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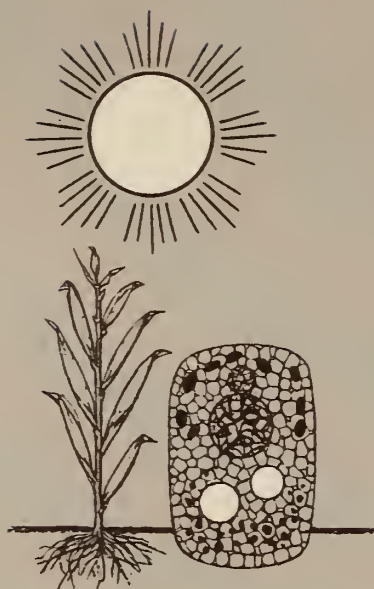
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The Emergent Viruses

During recent years the increased importance many countries attach to combating livestock diseases and the growing assistance to governments from such sources as the Food and Agriculture Organization of the United Nations have brought within measurable distance the control of some of the traditional epizootics.

Diseases which have caused famines, disrupted agriculture, and exerted a baleful influence on history now appear to be on the way to obscurity.

Such hard-won successes, unfortunately, are offset by the ominous emergence of a group of virus diseases—some of which already constitute major threats to livestock populations. Diseases such as African swine fever, African horse sickness, Asia-1 type foot-and-mouth disease, and others are finding chinks in our quarantine armor and are showing increased incidence in previously clean areas.

The time has come for a reappraisal of quarantine methods and means of sanitary control. In these days of rapid and efficient transport and large-scale movements of personnel and freight, we must face the fact that—more than in theory only—any disease may be transmitted to *any* part of the world.

Nomadism, clandestine contraband movements, the carrier animal, the “mechanical” conveyors—which may be foodstuffs, fomites and anything that moves, including man and his means of transport—are all involved in the new and critical challenge of disease.

The public health authorities who deal so efficiently with the six quarantinable diseases (plague, cholera, yellow fever, smallpox, typhus, and relapsing fever) in one animal species—man—are objects of professional envy by their veterinary confreres, who have to consider a multitude of potential epizootics, seven common animal hosts, and an unnumbered total of other active or potential carriers or hosts.

W. ROSS COCKRILL

*Food and Agriculture Organization
The United Nations, Rome, Italy*



Computer Applications to Agricultural Experimental Data

G. W. Gorsline

The trend towards collection of voluminous data in agricultural research can be laid to developments in many interrelated as well as seemingly independent fields. The continual development of statistics and the revolution in instrumentation have probably been only partial reasons. It seems evident that a more cogent reason has been the rapid development of the many sciences basic to agricultural research and the team approach to the more basic and difficult problems. Most present day North American and European agricultural laboratories and university departments are at least aware of the evolution, availability, and utility of the electronic digital computer for data manipulation and statistical reduction. That the application of computers to the solution of agricultural research problems has been less than satisfactory is attested by the fact that, with notable exceptions, graduate students use computer facilities more than their own major professors.

TYPES OF COMPUTERS

The term computer has a wide range of meanings, but usually means a device that solves a complete mathematical problem in contrast to an adding machine, slide rule, or other device that produces the result of only a single arithmetic operation. Computers can be classified into analog computers, digital computers, or hybrids of the two.

An analog computer directly simulates individual mathematical operations, such as multiplication or integrations, by connecting together a number of multipliers or integrators in an appropriate manner. Analog computers may have advantages in cost and speed for certain types of problems, notably differential equations. When the analog computer is applicable to the problem, the cost and speed advantage may apply to both the machine and to the work required to prepare the problem for solution. Often serious problems of accuracy not wholly solvable are associated with analog computers.

A digital computer uses numbers or coded numbers (usually a base 2 number system code) to represent the variables undergoing calculations. The basic ability of the machine is most often limited to the simple arithmetic operations of addition, subtraction, and replacement, as well as distinguishing number matches. The problem is solved by breaking it down into a succession of the basic operations called the "program."

The concept of the "stored program" that can be altered as the result of intermediate answers is basic to operation of a modern digital computer. Program production has been facilitated by the development of languages resembling algebra and, recently, the specialized jargon of various other fields. Programs written or "coded" in these "source" languages are translated or "compiled" into "object"

code by other programs called "compilers." Object code is expressed in the basic hardware notation of the particular computer.

The advantages of the digital computer include applicability to an extremely wide range of problems, limited mainly by the ability of the programmer to logically analyze the process and code it in a source language. Accuracy can be very good or poor depending on the computer, the method of solution chosen, and the digits employed in the arithmetic. The arithmetic of the digital computer is finite, in contrast to the infinite arithmetic commonly taught in high school and college to non-specialists. Resulting roundoff or truncation errors may even invalidate results in some techniques unless care is exercised in the choice of procedures.

Hybrid computers consist of various combinations of digital and analog components. In many cases, an individual hybrid machine is conceived and specially built to accomplish a specific purpose. Recently, components and the necessary electrical "interfaces" have become available to the extent that specialized dual machines can often be conceived and plugged into larger components to arrive at the desired capabilities. Hybrid computers are becoming important in biology and medicine; their use in agricultural research will undoubtedly increase.

This survey paper is restricted to a discussion of the use of digital computers in agricultural research. Although analog and hybrid computers have obvious application to specific research problems, their use will not be covered.

THE COMPUTER AND RESEARCH

Advantages of digital computer solution of research computational problems in agriculture must include at least:

- Accuracy of data manipulation.
- Speed of analysis allowing more time for interpretation.
- Analysis of all data.
- Economy of data manipulation.
- Treatment of problems not solvable by hand methods.

Extremely large memory or high speed arithmetic is not an inherent prerequisite for solving agricultural and biological problems. Although size and speed in computers are normally correlated, it does

not follow that "monsters" are necessary. For instance, at this time more data reduction and statistical techniques are coded for the IBM 1620 and for the IBM 1401¹ than for any other computer. Nevertheless, advantages of size and speed in computers include the following:

First, man-machine communication is easier because the computer may be programmed to interpret notation more appropriate to the problem.

Second, they are more flexible and therefore provide a more suitable format for input of data and output of results.

Third, economy is greater—at least from the individual problem standpoint.

Fourth, they are capable of man-machine-problem interaction on a real-time basis.

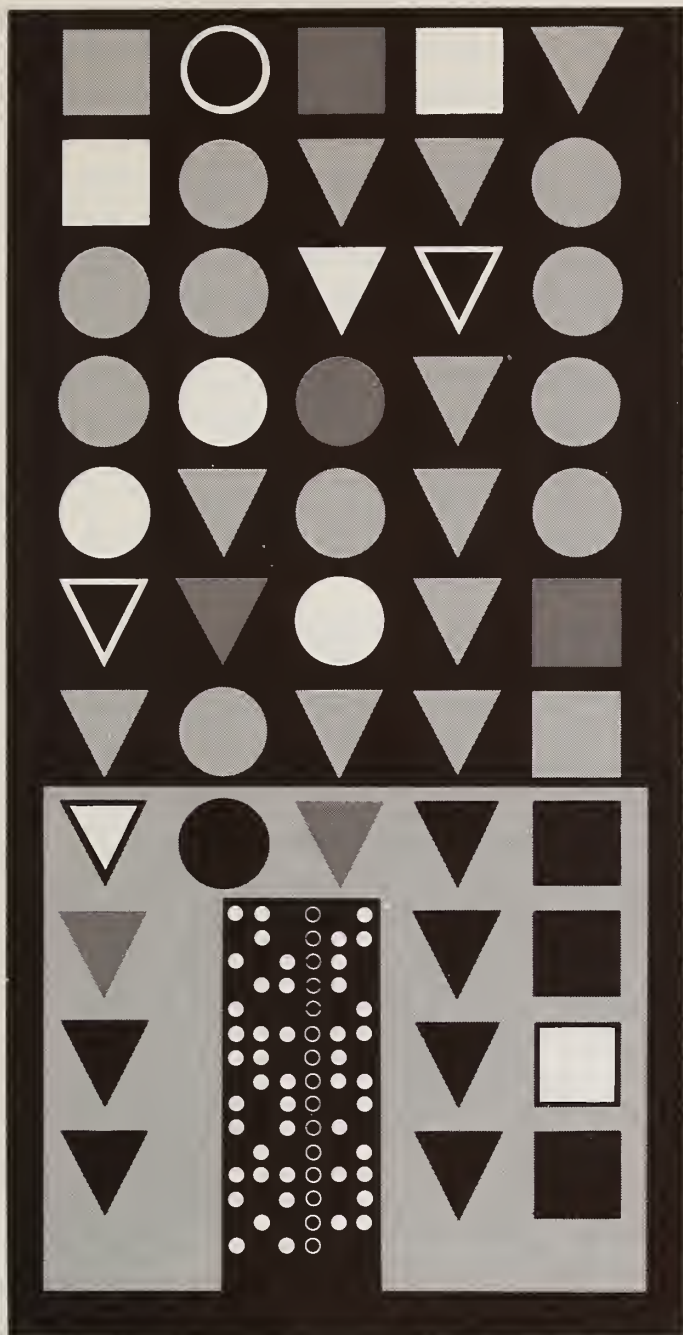
Fifth, they have the ability to solve a problem in "one pass" since large memory or programming in sections (segmentation or chaining) may allow the necessary program, summarized data, and intermediate answers to be contained at one time. Judicious programming may allow a small computer to use magnetic tape or disk storage to partially overcome size limitation, although trained programmers thoroughly familiar with the particular installation are usually needed.

Finally, fast problem "turn around" is usually possible with a fast computer, with an "executive" or master control program, and with proper organization—thus allowing return of results in a fairly short time (measured in hours and preferably half-hours).

Computer facilities are commonly organized in one of three ways:

1. *Closed Shop*—Professional computer personnel completely handle the data from the field or laboratory record sheets through the completed analysis. The time from submission of data to the return of results is rarely below a period of days and commonly may be a month or more. In addition, some man-data interaction is very often lost and possibly fruitful paths of investigation missed.
2. *Open Shop*—An individual investigator completely handles data preparation and opera-

¹ Trade names are used in this publication solely for the purpose of providing specific information. Mention of trade names does not constitute guarantee or warranty of the product by the U.S. Department of Agriculture or an endorsement of other products not mentioned.



tion of the computer. Since the data are always physically in the control of the investigator, no turn-around time is necessary and each implication of the data is at least available for notice. This situation is usually limited to smaller and slower computers.

3. *Semi-Open Shop*—An individual investigator prepares or oversees preparation of his data but the computer itself is operated and controlled by professionals. Most research-oriented university facilities with newer and larger computers have evolved to this situation. Turn-around time of much over 48 hours is commonly considered intolerable. Service is expected overnight or sooner depending on problem size and computer time required.

Hierarchical memories of extremely large size that are usable with intelligent programming are now available with acceptable speeds. This development, coupled with practical communication channel facilities, probably means that real-time problem solutions with large computer capabilities are available at practical cost to all researchers.

PROGRAMS

In the application of computers to agricultural and biological research, it has become evident that three classes of problems are describable.

Class I Programs

This class includes those problems with recurring data transformation, reduction, and semi-interpretative processes for which the procedures have been more or less fully developed. Programs to accomplish these objectives are in existence at most computation centers. Examples include data transformation, the analysis of variance and covariance, t-test, correlation, regression, partial regression, discriminant analysis, principle components analysis, curve fitting, and surface fitting.

At some computation centers Class I programs are referred to as "canned" programs. Following is a rough classification of known canned programs available at many computation centers and available for sharing.

1. General Statistics

Statistical summary

Normality of distribution

Frequency analysis

Bartlett's test of variance homogeneity

2. Correlation Analysis

Pearson's product moment correlation coefficient

Average and Test "r" differences by "z" transformation

3. Regression analysis

Linear regression coefficient

Scattergram graph

Polynomial equation derivation—to solve either of the functions:

$$Y = C + b_1X + b_2X^2 + \dots + b_nX^n$$

$$Y = C + b_{a1}X_a + b_{b1}X_b + b_{c1}X_aX_b + b_{a2}X_a^2 + b_{b2}X_b^2 + b_{c2}X_a^2X_b^2 + \dots$$

Empirical polynomial approximation of unknown functions is useful in describing instrumentation relationships, in identifying experimental background noise, and in finding data anomalies.

4. Multivariate analysis

Multiple regression—to solve the function:

$$Y = C + b_1X_1 + b_2X_2 + \dots + b_nX_n$$

(using matrix algebra and based on one of three assumptions). One type operates by building an equation with all variables ($x_1, x_2, \dots, x_n$) and then eliminating them by parsimony one at a time in reverse order of importance. The opposite type operates by building an equation with the one most important variable and then adding variables in order of importance. Neither of these approaches will necessarily result in the "best" equation (2).² The faster and larger computers are fully capable of the repeated trial and error procedure. Either of the above approaches is used as a starting point to arrive at the best equation by simply looking back at each step and checking the independent variables again.

Principal components analysis or factor analysis

Discriminant analysis and classification

5. Chi-Square Techniques

Chi-square contingency table

Chi-square fit to theory

6. Means Comparison Techniques

"T-test" programs—paired or unpaired

Mann-Whitney "U-test"

Duncan's multiple range test—using Hartner's revised tables

7. Analysis of Variance and Covariance

Of all statistical procedures, perhaps more programs are available to analyze data under various assumptions and designs of the analysis of variance and covariance than any other. Designs such as randomized complete block, Latin squares, lattices, and lattice squares are available. Programs are available for the analysis of

variance and covariance of the generalized factorial of various levels with varying numbers of subsamples and with and without missing cells.

Many analyses of variance programs have provisions for extracting linear, quadratic, and cubic components. Computer techniques should allow the extraction of additional terms and on any basis; that is, polynomials of any degree and dimensions including hyperspace. Approximations of theoretically suggested curval relationships should be practical. In the analysis of covariance, computer techniques should allow as many "x" variables (dimensions) as needed in any degree or combination of degrees justified.

Among recent developments, AARDVARK—the macro system of the Iowa State University Statistical Laboratory—builds the appropriate proportionate analysis of variance or covariance, or both, to 12 factors with specified restrictions starting from modified statistical notation (5, 6). It is expected that this or similar techniques, upon full development, will allow analysis of experimental designs of a rare or semi-unique nature in a semi-automatic way and facilitate statistical research.

8. Data Display Techniques

X-Y Plotters with digital, analog, or combination control are produced by several reliable corporations. Accuracy, precision (repeatability), and speed are complex functions in an indeterminate equation with price. Most computational facilities have available data display subroutines to visually display printed approximations of X-Y curve plots or X-Y-Z plots as contour maps with controllable scales and symbols. Display tubes of a useful size that may be photographed are becoming available as a feature of many computers.

9. Mathematical Techniques

Almost every computation center has a myriad of programs to accomplish most of the common and many of the more difficult mathematical techniques.

Class II Programs

This class includes those less common, but recurring, fairly well defined problems where the al-

² Italic numbers in parentheses refer to "Literature Cited" on page 10.

gorithms may not be completely generalized and in which the algorithmic coding requires less time and effort than the individual problem would require if done by the desk calculator. Examples are diallel analysis, Powers' genetic methods, the components of genetic covariance methods of the North Carolina School, and numerical taxonomy.

Class II programs exist at most computation centers. A complete listing is impossible by the very definition of such programs. Examples include the soil test interpretation programs of Iowa, Michigan, and Wisconsin; and DHIA program of Pennsylvania, and the specialized genetics and breeding programs of which those of Hicks,³ White,³ and Gorsline (4) in Pennsylvania are specifically known to this writer.

Most Class II programs will be conceived as a response to the need to reduce data from specific experiments. In a great many cases the algorithmic development and system of attack is a simultaneous mental contribution of the research team member most directly involved. Coding of the computer language and debugging is also most often done by this same person and his collaborators. In a few instances, notably the facility of the Beltsville USDA Station, the entire process from algorithmic development through coding and debugging is done by professionally trained people not a part of the research team.

All programs and their contained algorithms must be checked by simulated data of some type. In many instances this process is straightforward and uncomplicated, although it involves time-consuming hand calculation of the test problem. All too often the judicious choice of test problems so as to cover all conceivable cases only proves the inadequacy of the algorithms for the general case or the false interpretation of the algorithms into the system for computational flow. The consequence of these two situations can have quite different effects. Misinterpretation of soundly-founded algorithms usually results in changes to tests and branches. The use of algorithms that are inappropriate usually have far reaching consequences and results in: (a) changing logical conditions, constants, tests, or branches, (b) a re-extraction of the offending algorithms in a form suitable to the general case, or (c) after failure

of the former two, the imposition of theoretical conditions limiting the overall solution to some specified subset of the desired generality and thereby limiting conclusions.

Class III Programs

This class includes those specialized approaches that are almost, or wholly, impossible without computer facilities which make available extremely fast arithmetic processes in conjunction with large memories. Although algorithmic coding may be lengthy, this class of problems was usually unapproachable by desk calculator methods. Examples at present include simulation of individual gene action and interaction by Gill (3), the cybernetics approach to evolution and to differentiation of Maruyama (9) and selection simulation of Martin and Cockerham (8). Future applications seem limited only by the imagination and ingenuity of the alert investigator.

Class III programs, as the classification is used here, are probably extremely rare. This type program was almost inconceivable before the mental gymnastics allowed by computers touched off the chain reaction of inspiration only now just starting to be exploited.

Harris⁴ of Iowa State (now at Dekalb Agricultural Association) has been simulating individual alleles segregating at multiple linked and independent loci for situations up to 40 loci by using binary notation in a basically decimal machine. The "almost here" appearance of computers with memories of up to 9 million characters, which may be manipulated as 18 million digits and hopefully as 144 million bits, will allow simulation of genetical situations of a complexity approaching simple organisms. This should allow simulation tests of basic theory.

Watt (13) has reviewed examples of imaginative data manipulation that resulted in meaningful forecasts of the results of various possible actions and which allowed intelligent choices to be made. He cited a study on New England river flow by Maass (7) in which the interactions of various controls and water use on the long range economic benefits were investigated; a study by Royce *et al.* (10) on the type of fishing gear that would result in the largest long-term salmon catch in northern

³ Private communications.

⁴ Private communication.

Washington waters; and a study by Watt (12) on the optimum combination of insect control measures for long range control in a balsam forest.

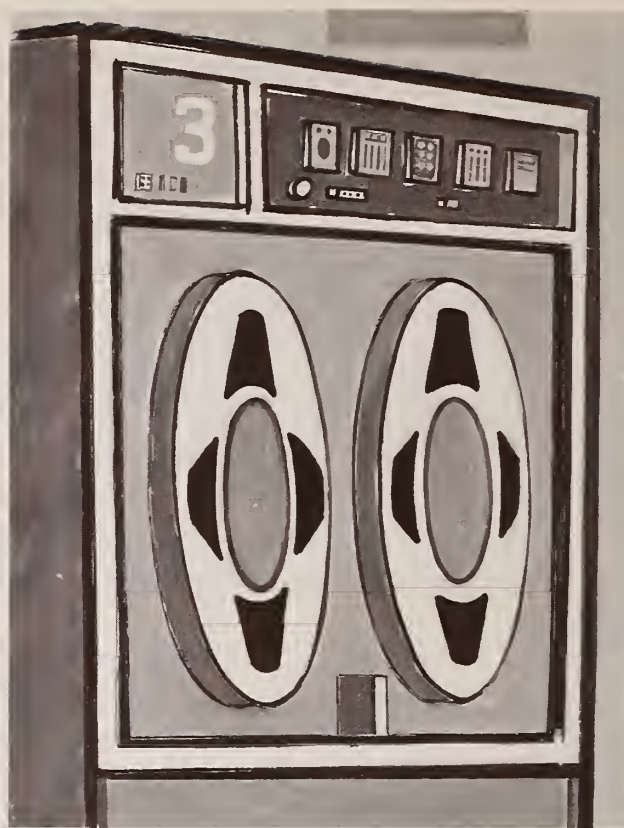
The cybernetical approach to evolution, organism growth, organism differentiation, organism development, soil genesis, and innumerable other topics is awaiting the marriage of mathematical treatment, theoretical imagination, and computational abilities. Numerical plant and animal taxonomy and soil classification may be closely related in methodology. Preliminary investigations suggest that setting up classification systems may be facilitated by the techniques of discriminant analysis as well as those of factor analysis in conjunction with multiple regression of the repeating type.

GENERALIZED vs. SPECIFIC PROGRAMS

When a programming specialist codes a program for use by many people, the strong tendency is to produce a procedure with as much generality as possible. An attempt is made to find or derive a method that does not fail with unusual data sets or values. Much effort is expended on producing code to check problem parameters and definitions, to check the intermediate answers so as to reduce roundoff errors, and to check the data for detectable illegalities and inconsistencies.

In attaining the desired generality, it is often impossible to include every path of analysis that may be desired for reducing specific or slightly unusual data. Provision is sometimes made for outputting the appropriate values for further special analysis. Nevertheless, the assumption that generality precludes specificity is usually true for computer programs. On the other hand, a majority of agricultural research data can be reduced and analyzed by one or a series of generalized programs available at most computation centers.

Specialized versions of the more common procedures may be useful and justified in some circumstances. Both an economic and a temporal question are directly involved. Much time and not a little direct expense are required in writing the detailed code, in debugging, and in running artificial test data through programs. If the same results can be obtained by the use of a series of existing programs, the production of the specialized program should be questioned. It should be pointed out, however,



that many specialized techniques have come into such common use that they belong in Class I.

PROGRAMMING

In practically all programs, the bottleneck in solving research computational problems is the coding of the algorithms into one of the formalized languages that can be translated by the computer into absolute machine language. Programmers, from analysts to coding clerks, are in extremely short supply and high demand. In addition, very serious problems of communication and understanding between divergently oriented individuals exist and seem destined to continue. It seems probable that the production of biological and agricultural computer techniques for extremely specialized problems will not be solved by computer professionals to a satisfactory degree. In examining projects active in computer usage, it is clear that in the majority of cases, the principle investigator or his collaborators have decided that a working knowledge of a problem-oriented computer language was necessary. Agricultural and biological research are not unique in this respect; nuclear physics, crystallography, meteorology, geology, and library science are experiencing the same trend.

At the present time, the FORTRAN or the ALGOL language seems to be almost universal for scientific problem coding. Most programs can thus be transliterated from one machine to most other machines. It is clearly evident that the development of the compiler to translate algorithms from the problem-oriented algebraic type FORTRAN or ALGOL language to a machine-oriented language and finally to the absolute machine instructions has allowed the research worker to take advantage of the speed, accuracy, and problem-solving power of computers. In such a situation, it becomes imperative that the computer solutions developed for Class I and Class II problems be made available to other investigators. Programs that fall into Class III may tend to be reclassified into Class II as agricultural science develops.

Happily, government, university, and an overwhelming majority of industrial computational facilities freely and readily make available programs that are not classified for security or business reasons. At present, four methods of reporting program development and availability are evident:

1. Computer manufacturers customer service publications reporting both system and applied programs. An example is the KWIK Index of the IBM Corporation.
2. User manuals of the various computation centers. Excellent examples have been developed by the computation center professionals at the Berkeley Campus of the University of California (1) and the Medical Center of the University of Cincinnati (11).
3. Word-of-mouth transmission among computer professionals and agricultural investigators.
4. Formal publication in agricultural and other journals of program descriptions and algorithms *per se* as incidental segments of research papers.

Programs developed in whole or in part with public funds, directly or indirectly, and not involving national security should be considered a part of the public domain and made freely available. Programs not involving industrial monetary protection should also be shared.

A formalized method of reporting program development and availability seems needed. Such a system would drastically reduce unnecessary program development and presumably result in saving

a part of the effort presently expended in unnecessarily coding existing programs. In addition a research worker would be aware of available programs and thus be in a position to take advantage of the efforts and ingenuity of other workers. Several requirements for the efficient functioning of such a reporting system seem clear at this time:

1. It must operate on at least two levels—for the professional programmer and for the active research worker in his particular specialty.
2. It must differentiate satisfactorily between those general statistical and mathematical procedures of interest to many fields and thus to the computer professional and those specialized procedures of interest to a specialized group.
3. It must be available in a usable style satisfactory to users at several levels of computer sophistication and agricultural research sophistication.
4. It must be easy to maintain and update without excessive cost, effort, time, delay, or red tape.

It is suggested that a first approximation of a workable system could be temporarily instituted as:

1. State-of-the-art review articles in an appropriate journal such as *Agricultural Science Review*. These might include a simple listing of advances in widely applicable programs such as defined in Class I.
2. Formal papers on research techniques on newly developed programs and algorithms of interest only to a specialized field. These would appropriately be published in specialized journals such as *Crop Science*. These reports on technique are on the same level and deserve the same journal paper recognition (with the same standards) as other papers on technique. It is suggested that each scientific society find a member reviewer who is a dual specialist—a professional both in the specialty science and in computer programming. This requirement is not an impossibility because at present most computer professionals have had primary training in other fields of specialization.
3. Each research report and paper that used computer programs in its preparation should give full credit to the appropriate program authors just as credit is given for other reports on techniques.

4. If new and unique computer programs and algorithms were developed to facilitate reported research, they should be reported and described in the appropriate part of the specialty paper.

TRAINING AGRICULTURAL SCIENTISTS

During the last several years, computers have become available to almost every agricultural scientist. Incredibly, their use spans the research life and training of over half of the agricultural scientists now active, but only a comparatively few have had formal training in their effective use. Part of the problem is obviously related to this short span of use. Computers have only been commonly available in the last 5 to 7 years, and their use in agricultural research spans approximately the same period.

Agricultural scientists should be trained in the use of the computer as a research tool, just as they now are trained in the use of statistics, the microscope, and other tools. Many scientists will have the inclination and the need to know more than others, but all should have a certain basic knowledge and experience.

This training problem logically devolves into three subproblems related to the career stage of the people involved—the practicing scientist, the graduate student, and the undergraduate student preparing for graduate work.

The practicing scientist can fairly painlessly acquire a working knowledge of an algebraically oriented computer language such as FORTRAN or ALGOL by attending short practically-oriented workshops held periodically by almost every computation center. The author has guided over 200 from diverse fields through such workshops. A certain attrition is inevitable, but it is usually true that university staff members are capable of completing a workshop equivalent to a freshman course. About 15 hours of lecture and 30 hours of practicum are sufficient. Alternately, many practicing scientists obtain self-teaching texts and successfully acquire a working knowledge of FORTRAN or ALGOL with very little help. Although self-teaching is practical, it is usually not efficient. A formal class or workshop should be substituted.

Many scientists will find that they need learn only how to use the available generalized pro-

grams. This includes becoming familiar with what programs are available, how to use these programs, and the procedures of the particular computation center. Usually a period of less than two hours is necessary to acquire this rudimentary knowledge.

Graduate students in agricultural science may become familiar with computers in helping process data of the supporting research project, in processing their own thesis or dissertation data, or in formal classes. Although many graduate students have learned programming and computer use through workshops or self-teaching books, this approach should be discouraged. Formal courses are commonly available on the concepts of computer usage, algebraic-oriented computer languages, and programming logic. It seems appropriate that all agricultural graduate students who would normally be required to study statistics also be required to schedule and successfully complete a computer programming course of 1 to 3 semester hours credit. It is considered essential that this course include both theory and practice in programming. A minimum of 8 to 10 programs should be successfully completed, at least 3 to 5 of these being moderately involved and difficult. The use of generalized programs and their alteration should be covered.

The vast majority of agricultural graduate students should not attempt to become experts in computers or languages. In other words, most scientists-in-training should learn to use a computer as a research and teaching tool within their field and not attempt to become computer professionals or quasi-experts. In practice this usually means a working knowledge of a problem-oriented language such as FORTRAN or ALGOL, but not of a machine-oriented language.

Undergraduate students preparing for graduate work could profitably gain their computer experience early in their undergraduate career. In addition, it is strongly suggested that a fuller grounding in mathematics be stressed in undergraduate training.

THE USE OF COMPUTERS IN CLASSES

A part of the training of advanced undergraduate and of all graduate students should be the use of the computer in agricultural classes to accomplish legitimate teaching objectives. Class problems

could be set up to accomplish the objective of the particular class, while demonstrating the utility of the computer and familiarizing the student with the procedures necessary to reduce data through the use of previously prepared programs. Use of computer techniques in statistics class after practice hand calculation of the identical procedures may be particularly appropriate. Dr. Dale Baker of the Agronomy Department, the Pennsylvania State University, is using a specially prepared program in an advanced laboratory course in soil chemistry involving knowns and unknowns analyzed on the flame photometer. Dr. Robert Hutton of the Agricultural Economics Department of the same university is using an advanced linear programming code in several formal and informal classes in farm management and economics with apparently great success.⁵ In the opinion of the author, the extension of this dual teaching concept can profitably be extended with benefit to the students of specific agricultural classes.

A LOOK INTO THE MISTY FUTURE

It seems obvious that digital computers are here to stay and that they are, and have been, a good

thing for agricultural research.

The experience of many people during the past several years suggests that research people use computers in a sort of evolutionary process. The first use seems to be simply to reduce and analyze data by using canned programs; which, by the way, is a laudable, justified, and necessary use. After a period of indeterminate length, most researchers come to realize the possibilities inherent in computer solution of more specialized and complex problems. Some investigators learn a problem-oriented computer language such as FORTRAN and proceed to take fuller advantage of the inherent power of the computer in their work. A very few theoretically alert and mathematically-oriented research workers take the obvious next step and begin to use the computer as a research tool in new and stimulating ways. Simulation, cybernetics, theory modeling and other as yet undefined procedures are being or will be used in basic research.

The use of computers as a tool in agricultural research at any or all levels is now an accepted procedure. Their use at any level of sophistication to better accomplish legitimate research objectives should be strongly encouraged.

GLOSSARY

Accuracy—the degree of exactness of an approximation or measurement.

Address—an identification for a register or location in storage.

Algol—ALGOritmic Language—a formal computer problem-oriented language by which problems may be presented to a computer.

Algorithm—the procedure for solution of a problem expressed in a notation amenable to numerical solution.

Analog computer—a computer which represents variables by physical analogies, such as electrical circuits, or an analog for the physical phenomena. Thus, an analog computer measures continuously, whereas a digital computer counts discretely.

Analyst—a person skilled in the definition of and the development of techniques for the solving of a problem.

Assembler—a computer program which operates on a program written in a machine-oriented language producing corresponding machine instructions.

Bit—BIInary digiT—a unit of information capacity of a storage device; a single character in a binary number.

Branch—the selection of one or two or more possible paths in the flow of control based on some criterion.

Bug—a mistake in the design of a routine.

Canned programs—(library programs) a collection of standard proven routines by which problems may be solved.

Cell—a location specified by whole or part of the address and possessed of the faculty of store.

Code—a system of symbols for meaningful communications. The coding of a problem involves the notation of an algorithm in the detail of a computer language.

Compiler—a computer program which operates on a program written in a problem- or procedure-oriented language producing a series of corresponding machine instructions.

Debug—to locate and correct any errors in a computer program.

Digital computer—a computer which processes information represented by discrete or discontinuous data. A stored program device for performing sequences of internally stored instruction causing arithmetic and logical operations to be carried out on internally stored data and possibly its own instructions.

Display tube—a cathode ray tube used to display information.

Error—the amount by which the computed or measured quantity differs from the theoretically correct or true value.

Execute—to interpret a machine instruction and perform the indicated operation(s) on the datum(a) specified.

Fortran—FOR TRANslation—a formal procedure-oriented computer language by which numerical procedures may be presented to a computer. FORTRAN allows algebraic-type representation of a problem.

Hierarchical memories—a series of hardware devices capable of storing information that can be found and retrieved at different relative speeds. The most expensive and fastest is immediate access memory or internal

⁵ Private communications.

computer storage. Others include magnetic tapes, disks, drums, and others.

Hybrid computer—a computer which is some combination of digital and hybrid components and which is thus capable of both analog and digital computer functions.

Input-output—a general term for the equipment used to communicate with a computer.

Instruction—a set of characters which defines an operation together with one or more addresses, or no address, and which, as a unit, causes the computer to perform the operation on the indicated quantities.

Interface—a common boundary between computer systems or parts of a single system.

Object program—the output of an assembler or of a com-

piler. The object program is usually machine language code ready for execution.

Precision—the degree of exactness with which a quantity is stated.

Program—the complete plan, or the preparation thereof, for the solution of a problem.

Source program—a computer program written in a language designed for ease of expression of a class of problems or procedures by humans. A compiler or an assembler is used to translate the source program into an object program.

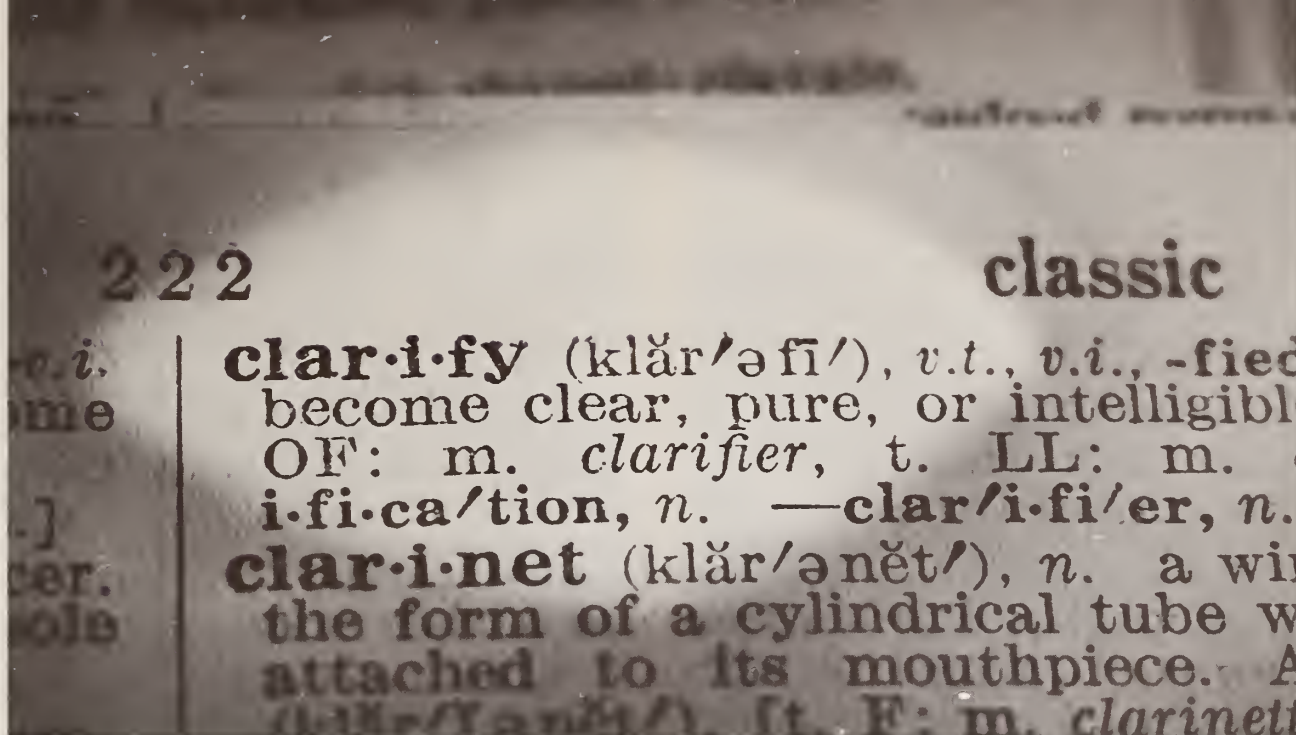
Stored program—a series of instructions in storage to direct the step-by-step operation of the machines.

Turn around time—the total elapsed time required for a computer run.

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LINGUISTIC BARRIERS IN SCIENCE WRITING

Russell G. Lynch

The following article represents a veteran newspaperman's approach to the perennial problem of communication in the world of science. Mr. Lynch has earned the respect of journalists and scientists alike, because of his constant attention to accuracy and clarity in science reporting. Winner of several writing awards, he also earned for his paper—the Milwaukee Journal—a merit award from the Soil Conservation Society of America. Here, in his typical succinct style, he deals boldly with the basic theme of achieving better communication between scientist and layman, and, indeed, between scientist and scientist. This article is based on a talk entitled, "Do They Dig You Daddio or Are You Way Out?" which the author gave at a national seminar on water resources problems.

Beatniks use a peculiar lingo which is meant to exclude others from their private little world. Some scientists and technologists are guilty of the same kind of snobbishness when they use jargon. The cost is a breakdown in communication which they can ill afford.

Jargon, however, is not the only barrier to communication, nor is snobbery the sole explanation for the use of words that convey little or no meaning to the average person.

Good scientific and technical terms, uncommon words and foreign expressions or quotations—all fine in the right company—can lose ordinary readers or listeners and may even antagonize them.

A British writer, Rebecca West, who has devoted much thought to the motivation of traitors, speculates that a certain type of scientist, because of his mastery of one field, develops a kind of intellectual arrogance. She was writing about nuclear physicists, but it is likely that this type of mind exists in other disciplines and may in rare cases account for failure to communicate.

More often, it is a feeling of inferiority that compels the use of important sounding words—a lack of confidence in one's material or the presentation of it.

Sometimes the one failing to communicate may be unconscious of his fault or only dimly aware of any such responsibility. Intense preoccupation with his specialty has isolated him.

Whatever the fault may be—intellectual snobbery or arrogance, fuzzy thinking or erudite ignorance—all of the guilty ones limit their usefulness and sometimes their accomplishments, particularly if they are in public agencies and emphatically if they are teachers, at any level.

Scientists and technologists are not the only offenders. Men with less excuse, because their business is communication, are guilty.

Reporters on scientific and technological matters must guard against a common failing—writing for the specialists instead of the public. Or they may simply start using technical words which become familiar to them. An able medical reporter for a newspaper was guilty of this. “Ingest” became one of his words. A simple word that anyone should know? Ask a few people. Why not use “swallow” and be sure that every reader will understand?

Newspaper and magazine writers, particularly columnists, like to show off a bit. They substitute ponderous words for simple ones at the sacrifice of communication, and sometimes they sacrifice the specific meaning of a useful word.

“Pragmatic” has been popping up in columns and articles. It is also a currently popular word among research workers. The diverse definitions of this word, particularly its intrinsic meaning, give it little utility. What these writers usually mean is “practical” and if they used that word their readers would not be wondering what they meant.

Similarly, the use of “anticipate” to mean “expect” has just about left us without any word to express anticipation.

The once-dignified word “research” has fallen into common use to give false importance to routine chores. On the jacket of a book recently offered for popular sale I read that the author had been in Europe for “auctorial research.” Advertising and promotion writers may be chiefly to blame for such misuse, but even men in science and technology abuse this word.

They are also whittling “parameter” down to a mere measurement.

At this point, readers doubtless are saying to themselves that this article was written from ignorance, and they are quite right.

A decade ago, I began to write about natural resources for the *Milwaukee Journal*—the first newspaper in the country with a full-time reporter in the whole broad field of resources. I attended meetings where scientists and technologists spoke, worked from their papers and summaries, and read extensively for background information. I had to give myself a short course in every new phase I tackled. For a while, I was depressed by my ignorance.

Then I realized that there was a very serious lack of communication between some scientific and technological people and the public. I realized that ignorance was an asset, because my task really was to interpret what these men said; to explain resource matters to people with as little grounding as I had, or less, and also more or less indifference.

Lack of communication is particularly serious in natural resource fields, where research and studies must solve problems or develop approaches to them. Men assigned to these tasks are too inclined to confine their discussions to the knowing circle. After they reach decisions or prepare plans, they spring their proposals on the public and expect them to be received gratefully and implemented. This seems to me a major reason why progress has been so slow toward wise management of resources.

It is important that the public be taken along on the whole trip. Usually some changes are required, support must be generated, money must be provided. People just do not accept changes unless they are convinced by good reasons. They or their representatives will not dig up money for things not understood. Except when they are frightened, I should say, and that provides a valid excuse for such a vulnerable document as *Silent Spring*.

Now, I do not want to be misunderstood. I admire fine writing and polished discourse. I understand and appreciate the need for exactness in scientific and technical terms. Friends in various disciplines have pointed out that scientific papers must be written so that scientists everywhere can understand and use them. Many research authors do this and at the same time communicate very well with the public. But some carry their jargon outside and use it in speaking or writing for the public. Then communication breaks down.

An example is “discipline.” I use the word here but I would not use it in a newspaper article. Stop 100 persons on the street and ask what “a discipline” is and I will be surprised if you get one right answer.

Even in their own meetings, scientists and technologists are sometimes less than comprehensible. At a luncheon one time, I sat with two technologists who talked two different dialects of the same jargon.

At a national seminar on aquatic biology that I attended, radioactivity was the subject of the first session. The “radiobiologists” talked a language that other biologists at times had difficulty in following.

TLM was one of the terms. A speaker, hearing the rustle of questions in the audience, explained that it was about the same as LD-50. Like others, I knew this meant the dose lethal to half an experimental population, so I groped along with the speakers.

On the way out, I asked a Ph. D. of my acquaintance what TLM stood for. He said, "Oh, about the same as LD-50." I said, "I heard the man, but what do the letters represent?" He laughed and said he didn't know.

Another man turned around and said, "Toxicity limit median, I think." A third man corrected him, saying, "No, it's tolerance limit median."

Subsequently I received notice of another seminar in California on "benthic biology." I looked in my *Webster Collegiate* dictionary and found "benthos" (in the new word section) defined as fresh water bottom-dwelling organisms. Then I lugged my big *Merriam Webster* to the dining room table and found that benthos was the flora and fauna of the sea bottom. Next I consulted encyclopedia at the office. *Americana* said benthos was the fauna of ocean depths under 100 fathoms; *Britannica* said it was the sedentary bottom-living animal and plant life of the sea.

And I said, "Why don't people say what they mean!"

I resent men who flaunt their erudition with frequent interpolations of exotic words where English would serve as well and with occasional whole paragraphs in text or footnote of untranslated Greek, Latin, French, and German.

Any man who has something of value to say, I think, does not have the right, ethically, to deny it to any mind capable of understanding the facts or the thoughts, simply because the possessor of that mind lacks his own high level education.

Such men seem to forget that semantics, too, is a science and communication an art. And *nothing* has contributed as much to the advance of civilization as communication.

Where one author deliberately throws up linguistic barriers for his inferiors, some others fail to communicate because they are mentally marooned on chosen islands.

A few years ago, a midwestern university published a remarkable work on the vegetation of its

State. Publication notice and book jacket said that the book was written with a minimum of technical terms, for the use of (among others) farmers, conservation workers and men in weed control and recreation.

The author really had me wearing out my dictionaries. I found 20 or 30 words in the first two or three chapters that were not in my *Collegiate*, and some were not even in the *Merriam*. I stuck with it and was well rewarded, but I wondered how many farmers, weed control men and conservation workers went beyond such expressions as "varietal endemism", "morphological subspeciation", "altitudinal retardation of phenological events", or "Gaussian amplitude curve."

How many readers will use a dictionary? Much less read with one at hand? And when the offering is oral, there is no dictionary and a man can lose his audience quickly.

A nationally known specialist on water resources recently addressed a Milwaukee gathering of conservationists. His paper was a polished masterpiece. My admiration was tarnished as I left the hall, when a lawyer commented, "I should have brought along a dictionary!"

Perhaps it is a good omen that scientists and technicians who understand the necessity of communicating with the public have become critical of their associates who ignore their responsibility.

Marston Bates, University of Michigan zoologist, referred in one of his books to a new word, "biocenosis", coined as a substitute for "community."

"Biocenosis," he wrote, "leads easily to biomes and biochores, to ecosystems and ecotones. These are all lovely words but they don't really say anything new. The trouble is that the word-coiner, sinking blissfully into his additions, gradually loses all communication with the outside world. He emerges from time to time to complain that the world doesn't really understand or appreciate his important thoughts—meaning his big words."

Joseph Hickey, a University of Wisconsin professor, while he was editor of the *Journal of the Wildlife Society*, told me he ran across such gems as this:

"While piloting a Polar Cub 30 miles west of Churchill, two foxes were seen in a highly abnormal condition."

Aside from indicating that two foxes seem to have been piloting an airplane, this was not very informative.

And this one:

"A porcupine covered with *Sarcoptes scabiei* was brought to the laboratory in a morbid condition."

That Journal once had a fuss in its letter column over editorial requests for polishing up manuscripts, which led Justin Leonard, assistant conservation director of Michigan, to comment:

"The Ph. D. in science can make journal editors quite happy with plain, unadorned, eighth-grade level composition."

Joseph P. Linduska, who edited the Interior Department's book, *Waterfowl Tomorrow*, of multiple authorship, had quite a struggle getting some of the contributors to use plain language, suitable for popular reading. The Agriculture Department doubtless has had a similar problem with its year-book.

As I explained to one of Linduska's authors, who sought my help, there is a simple rule: If an ordinary reader would have to look up a word, look it up for him and use the commonest synonym in the dictionary. Most readers won't bother; they will pass over the word or pass up the article.

They might not be helped by a dictionary in some instances. Example: "Soil amendment." Soil scientists like to use this one—probably to add a touch of dignity to earthy things. In a technical publication, it's probably all right. But the plain truth is that they are talking about fertilizer.

Scientists, particularly those in academic circles, are very wary of newspaper reporters. They are fearful of being made to "look bad", one explained to me. Look bad to whom? Surely not the newspaper readers in general? And just as surely not to fellow scientists, who will know that any fumbling was the reporter's, even if they do rib the victim.

If a scientist has a story that should interest a fair segment of the public, he should be glad to give it to a reporter. He has a right to ask the editor for a conscientious reporter if he does not get one the first time. He should take pains to see that the reporter understands the facts (a good reporter will see to that himself). If something is wrong when the story appears in print, this should not call forth anguished outcries but rather lead to a friendly and helpful explanation of where the writer went wrong.

This attitude can be very rewarding both for the individual scientist and for fellow scientists who may find that reporter useful.

As a reporter, I was fortunate to get such help from scientists and technologists well equipped to communicate. I ran into others, typified by a man who was asked to check the irrigation section of a report I wrote on Colorado river salinity problems. My task was to make it simple enough to appeal to newspaper editors. The expert found it "difficult to review" because it was "oversimplified."

Watson Davis, director of Science Service, in an address some years ago at a scientific communication conference held by the American Association for the Advancement of Science, said this:

"The great art in telling is to make the words mean what you want them to, not in your own mind but in the minds of others. There is little need for 'writing down'. This is demonstrated by the daily newspaper which serves children and old folks alike. Clearness and vividness are more needed than vocabulary limitations based on word lists."

Given the chance, I think that I could convince Mr. Watson that vocabulary limitation is necessary—not in the concept of "word lists" but in bilingual ability.

Scientific terms and the popular tongue surely are two different languages. The "great art" is, as Mr. Watson said, to make words meaningful in the minds of others. The simplest way, and really the only practical one, is to talk the other man's language. The alternative is to interpolate frequent explanations to make scientific or technological words meaningful. A little of this is good; too much will bore the listener or reader, if it does not affront him.

As for "writing down" (or talking down), it is dangerous even to think in such terms. Remind yourself that in the present state of biological evolution the people you address are apt to have minds as good as yours. They just lack the tools to use their minds as you use yours. Your job is to supply the tools.

Words are the tools of the mind. It has been written that man was unable to think much better than lower animals until he provided symbols and then words.

Ask yourself what your objective is. To impart knowledge? Or to parade knowledge?

If you want people to think about things that concern you and your work, use words they know or supply new, useful words. Do it casually, not in a

way that seems to say, "See how much more I know than you do!"

The author of the aforementioned book about a State's vegetation occasionally tried to do this. He used "podzolization" with the explanation that it meant topsoil impoverishment by leaching and translocation. But he needed simpler words even in his explanations.

I heard some years ago about a game biologist, talking to a group of farmers. He got off a string of big words and knew from the facial expressions that he was over his listeners' heads. So he said, "I won't attempt to explain that; you wouldn't understand it anyhow." Right there he lost them beyond recall.

Be sure, if you are talking or writing "down", people will get the message just as plainly as those farmers did, even if you don't do it as crudely as that.

As a writer or speaker, you should recognize that three areas of communication call for different efforts:

1. Your own group or discipline.

You may expect the language of a discipline to be familiar to its disciples, but not the jargon, or oral shorthand, of a specialized group within the discipline.

2. Others who may want your information and can be expected to put forth a reasonable effort to understand.

Some of the burden of communication may be placed on these people, but not all of it. You may make them reach a bit, expect them to ask questions and look up things. But a good writer or speaker will take on more than his share of the burden.

3. Those you want to interest, or should, but who lack the specialized vocabulary.

This group comprises most of the people to whom a man in the public service must address himself, from citizens to legislators. The burden of communicating is entirely on the writer or speaker. He must assume that only fairly common words will convey meaning and, in speaking, be alert for signs that the audience is not following him.

If you accept the duty of communicating and work at it successfully, more of your material will get into newspapers. Competition for news space is murderous. The editor's waste basket is large and his reporters' assignment sheet is crowded.

If your press releases do not get into print, if reporters do not come to your meetings or, having come, walk out and print nothing, examine your efforts.

Maybe your papers are too full of the kind of language I have described, or your summaries, which usually are more useful to the press, are equally foggy. I think that authors should not prepare summaries. That is a job for an interpreter.

In my observation, communication is much more effective if a press relations man is a good newspaperman who can pick up the scientific or technical knowledge he needs, rather than a scientist or technologist who may never be able to understand the newspaper business or what may seem to him its senseless whims.

At the aquatic biology seminar mentioned earlier, some papers contained material bound to interest large segments of the public, but it took some winnowing and translating. So the only local newspaper coverage was in the form of interviews with a couple of guest speakers from the conservation field, Ernest Swift and Seth Gordon. The interviews had very little relation to the seminar program but gave the newspapers a chance to get the seminar into their columns.

Later, at the National Conference on Water Pollution, there was a wealth of good material buried in the papers of top-ranking scientists and engineers. But it was what I said as leader of a panel on "Public Awareness and Citizen Responsibility" that provided the Associated Press with a lead for both its day and night stories.

In both cases, reporters used material they knew would be understandable and perhaps interesting to their readers.

Readers of this article, I am sure, have seen similar occurrences. They are food for thought rather than cause for chagrin.

People are not compelled to listen to you or read your papers. You are in a buyer's market, competing with murder, rape, politics, lukewarm war, aerospace travel and comics in the newspapers; entertainment on television; and sex, whodunits and westerns on drugstore book counters.

At the very least, you must make what you say understandable, and if you have the talent you had better make it interesting, too.

Regard it as a challenge, for that it surely is!

Somatic Chromosome Reduction

As a Tool in Plant Breeding

J. G. Ross



Plant breeders have long dreamed of an easy method of inducing immediate homozygosity in plants, so that new varieties or inbreds might be produced immediately. The use of naturally occurring haploids by doubling their chromosome number has been at best a fortuitous and undependable method to achieve this end. Likewise, efforts to induce the female or male gametes to develop embryos at will have not been successful as a practical technique in plant breeding.

As an alternative to the above, Huskins (21)¹ in 1948 pointed to the possible production of homozygous diploids from doubling of haploid cells, which had been induced by chromosome reduction within somatic tissue, and indicated the possibility that this could be a valuable potential tool in plant breeding. Though cytological evidences for the occurrence of reductional groupings were observed,

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¹ Italic numbers in parentheses refer to "Literature Cited" on page 24.

well founded evidence for the induction of tissue derived from such a reduction of chromosomes was not found. In 1952, however, Franzke and Ross (12) and in 1954 Ross *et al.* (31) interpreted the appearance of immediately true-breeding diploid mutants in sorghum after colchicine treatment as genetic evidence for the occurrence of somatic chromosome reduction. This paper reviews the evidence for this interpretation, as it has been uncovered during the ensuing years, and deals with the application of this phenomenon in the sorghum breeding program at South Dakota State University.

Naturally Occurring Somatic Reduction

In a succinct discussion of observations relating to evidences for somatic chromosome reduction, Swanson (38) mentioned the occurrence of somatic reduction as an integral part of the metamorphosis of the mosquito. Giant polyploid cells were found to undergo distinct reductional divisions which resulted in drastic reduction of ploidy within the resultant cells. Somatic reduction divisions within the gonads of hermaphrodites of the cushion insect

Icera perchesi must also have occurred to give the haploid somatic cells observed in these organs. These haploid cells were found to contain the complete haploid complement, but the mechanism by which they occurred has not been discovered.

In liver cells of the rat Gläss (17) identified complete genomes in groups separated from the rest of the chromosomes. Mitra *et al.* (27) have noted the presence of haploid cells in tissue cultures of diploid cells of the plant *Haplopappus*. Haploid cells have also been recognized in tissue of other diploid organisms.

Huskins and Chouinard (22) found triploid and diploid roots and a diploid shoot growing from a tetraploid *Tradescantia*. In complex allopolyploids of *Gossypium*, branches were observed which contained reduced numbers of chromosomes (26).

The mechanisms by which somatic chromosome reduction occurred in the above cases, except in that of the mosquito, are not understood.

Induction of Somatic Reduction

Huskins (21) observed the separation of chromosomes into groups after treating onion root tips with sodium nucleate. He interpreted this as evidence for the induction of somatic chromosome reduction. This phenomenon was later designated as reductional grouping, since a mechanism determining its occurrence could not be detected. Separation of homologues into different groups in a greater frequency than would be expected by random separation was noted. An "homologous repulsion" to explain the greater than expected separation of homologous chromosomes was postulated.

After treating sorghum seedlings with colchicine, Franzke and Ross (12) and Ross *et al.* (13) noted that, instead of the classical polyploidizing effect, diploid mutants were induced. Some of these mutants bred true immediately, while others segregated for the changed characters. The immediately true-breeding nature of the mutants was explained by proposing that a somatic chromosome reduction had occurred and that a cell so formed could form a new growing point. Such a cell must have had a genotypic and positional advantage to allow this to take place. The changed genotypes of the mutants were considered to have occurred as a result of a concentration of chromosomes from one of the original ancestors of the putative allotetraploid

containing two sets of chromosomes, each from a different ancestor. To test the hypothesis of somatic chromosome reduction, readily available genetic and cytogenetic markers were used which had been well characterized in other species. Such markers made it possible to distinguish members of homologous pairs so that separation of homologues could be detected. Even if the diploid condition may have been restored by doubling of the chromosomes in a haploid cell derived by somatic reduction, such markers would establish its occurrence.

In corn, structural chromosome markers in the form of interchanges were used. From treated seedlings carrying heterozygous structural markers on two pairs of chromosomes, nine survivors were studied. Two of the nine were homozygous; another plant had a heterozygous tiller and a homozygous tiller as determined by examination of pollen mother cells. In one instance identification of the chromosomes was possible and indicated homozygosity for the male parental form. Unfortunately, study of the next generation was not possible because of heavy smut infection. The 15 untreated plants used as controls were all heterozygous for the markers. Failure to induce the phenomenon was encountered when this experiment was repeated.

When similar structural markers were used in barley and in other varieties of sorghum, the phenomenon was not observed. However, success was achieved in flax when a gene marker was used (7). In a treated F_1 plant originally heterozygous for seed and flower color, 3 branches with blue flowers and brown seeds, 2 with white flowers and yellow seeds, and one a chimera of these two tissues were observed. Since the genes for these two characters are either very closely linked or the characters are affected by the one gene, at least the members of one pair of chromosomes would appear to have separated and afterwards to be restored by doubling to the disomic condition.

Demonstration of Somatic Reduction

It was concluded that, since the phenomenon was peculiar to certain genotypes, it would be necessary to work with a "reactive" genotype. A differential reaction to colchicine treatments was found between the genotypes of the variety Norghum and the variety Experimental 3 in which the phenomenon had first been observed (1). Experimental 3 was

an unreleased variety originating from crosses between forage sorghums and grain sorghums. Norghum on the other hand had only grain sorghum in its ancestry. To obtain structural markers on the chromosomes, irradiation of panicles of the reactive genotype, Experimental 3, was made just prior to anthesis. Irradiation of seed of this variety had previously been found to be unsatisfactory from the standpoint of yield of interchanges. Three chromosome interchanges, one involving the nucleolous chromosome, were found and described (20). These interchanges in the homozygous condition were used in crosses to obtain F_1 embryos heterozygous for the structural chromosome markers. Since a portion of a chromosome from one homologous pair was interchanged with a portion of a chromosome from another pair, the presence of such an interchange could be detected in the heterozygous condition by examining pairing relationships at prophase of meiosis. Attraction and chiasma formation between homologous regions located in each of 4 different chromosomes gave a ring or chain of 4 chromosomes easily recognizable at the diakinesis stage of meiosis.

Three hundred and twenty seedlings heterozygous for markers on 2 pairs of chromosomes were treated with colchicine, and 4 homozygous mutants were found among the 188 survivors (35). These four mutants were shown to be homozygous for normal chromosome structure identical to the male parent and, therefore, selfing could not have accounted for their appearance. In addition to the 4 homozygous mutants, 4 progenies were found which contained mutant and normal genotypes, indicating that the parent plants were chimeras. The 92 survivors of the 117 heterozygous seedlings used as controls were semisterile as expected in heterozygous interchanges and showed no variation in genotype as indicated by their progenies. The efficacy of the technique of treatment was estimated by treatment of normal Experimental 3. Eight mutants were observed among the 49 survivors of the 76 treated seedlings.

Although, as indicated above, origin of the structural homozygotes from the unfertilized egg could be ruled out, the possibility that the sperm could have given rise to the homozygous plants was not excluded. Therefore, crosses were made between homozygous interchange lines to give heterozygotes

with structural chromosome markers on four chromosomes (36). It should, therefore, be possible to obtain through somatic chromosome reduction, a homozygote for normal chromosomes different than either parent. This condition was found in the 2 mutants occurring among 90 survivors of 124 seedlings treated with colchicine. The possibility, therefore, of either the egg or the sperm having formed an embryo through an apomictic process was excluded.

On the basis of these results, it must be concluded that a reduction division of at least the members of 4 marked chromosome pairs out of the 10 has occurred after colchicine treatment of this genotype of sorghum—under the conditions of these experiments. The occurrence of normal chromosome structure in each instance may indicate a selection for cells with this chromosome organization. Presumably, the most viable genotype available in the region of the apical growing region would proliferate to form the new growing point.

Induction of Reduced Ploidy

If somatic chromosome reduction actually occurs after treatment with colchicine, it should be possible to treat tetraploids and obtain diploids and also obtain haploids in some instance after treatment. Finding tetraploid forms as well as diploid mutants of the Experimental 3 genotype after colchicine treatment provided a means of testing this possibility. Treatment of 20 tetraploid seedlings gave 9 survivors of which 5 were diploids (32). Four had normal meiotic behavior, while the fifth was later shown to have behavior typical of cytoplasmic male sterility. Fifteen of the 20 control plants survived and all were tetraploid. Other tetraploids of a different but related genotype were treated with colchicine in a later experiment (4). These were found in a tetraploid portion of a progeny from a plant treated with colchicine after previous treatment with ethylene amine. The genotype was vastly changed from tetraploid Experimental 3 since it segregated for awns, height, seed color and was much more fertile. Three diploid mutants were found among the 4 survivors after treating 20 seedlings. All of the 39 control plants were tetraploid.

Haploids have been noted in a number of instances after colchicine treatment of other species

than sorghum, but their occurrence was not associated directly with the colchicine treatment. In most instances the haploid seedlings were considered to have been haploid before the treatment. In one experiment designed to demonstrate somatic reduction using marked chromosomes, a haploid mutant was found after treating normal Experimental 3 (37). Because of the rigorous selection of large seeds, elimination of any seedling with double embryos and, also, the highly lethal effects of treatment (only 4 out of 20 treated seedlings survived), it was concluded that a haploid seedling would not have been treated with colchicine and would certainly have perished even if treated. It was considered, therefore, that this haploid resulted from the treatment. This conclusion was further corroborated when genetic tests showed that the mutant genotype was identical to white seeded mutants previously obtained after colchicine treatment of Experimental 3. It should be emphasized again that mutants have not been observed in untreated Experimental 3.

Nature of Mutational Effects

As indicated above, the mutational effects were first attributed to a concentration of chromatin from one of the ancestors. If this were so, then homology between chromosomes should be detectable by observing pairing relationships at prophase of meiosis. Homologous chromosomes normally pair together and remain loosely associated by means of chiasmata during prophase. Associations only in pairs were found at meiosis in the original genotype, in the mutants, and also in F_1 hybrids involving the mutants and the original genotype (19). The changes, therefore, appeared to be due to true gene mutations.

Studies of the segregation of changed characters in F_2 populations of crosses of various mutants with the original genotype indicated that the mutated genes were not linked and that they were inherited in a Mendelian fashion (9, 10). Some were qualitatively inherited and others quantitatively. In two instances, cytoplasmic male sterility was defined in mutants appearing after treatment, indicating that changes in cytoplasmic inheritance as well as nuclear inheritance can occur. At least 12 genes had been mutated to give 6 changed characters in a grass type mutant (11). Other characters be-

sides those studied had also been changed, so that a wider spectrum of changed genes actually occurred than the study indicated.

Radiation of the reactive genotype with gamma rays did not duplicate the effects of colchicine (18). Single gene changes occurred which were detrimental in their effect, in contrast to the colchicine changes which increased the vigor in some instances.

In certain respects the original hypothesis involving chromosome substitutions from one set of chromosomes to the other explains the experimental data very well. Substitution would explain how identical spectra of mutations could occur (6) and also how new mutants might arise after treatment of previously-induced mutants (13). The different classes of mutants observed after colchicine treatment could be explained by the substitution of a specific chromosome for each class from one genome to the other (14, 33). The cytogenetic data, however, do not affirm this hypothesis, since evidence for homology between pairs of chromosomes has not been found. Even if a gene were present in sorghum which caused chromosomes to be associated only in pairs so that homologies between pairs could not be detected, it would be expected that a bivalent or bivalents would consistently be found at prophase of meiosis in a haploid mutant. Examinations of a colchicine-induced haploid mutant and naturally occurring haploids of Experimental 3 and other unrelated genotypes were made recently. Bivalents were observed in a small proportion of cells in each instance, but no increased association of chromosomes in the mutant over that observed in the other haploids was noted. This was contrary to what would be expected if the mutated characters arose through substitution of chromosomes from one genome to the other.

Instances of mutations from recessive to dominant forms have been reported (6, 14). Purple spots on the leaves, dominant to absence of spots, were found in grass-type mutants. The expression of purple spots has been maintained irrespective of the genetic background on which the gene occurred. It is difficult to explain mutations to the dominant form by the chromosome substitution hypothesis.

The recent demonstration of homozygous mutants in barley after colchicine treatment (16) cannot be explained by chromosome substitution, since barley is not allotetraploid.



FIGURE 1.—The chromosomes above are a perfect pair; only the genes they carry are different. Before the cell can grow, each chromosome duplicates itself. Fibers form from the cell wall.

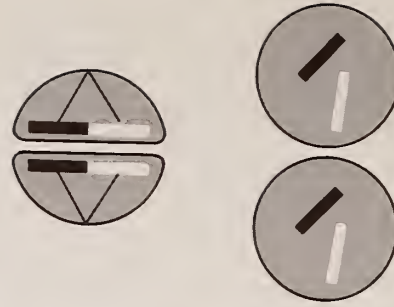


FIGURE 2.—The fibers pull identical chromosomes away from each other and walls grow between the new cells. These “daughter” cells will soon start a division of their own, thus plant grows.



FIGURE 3.—Even after the cell is treated with colchicine, chromosomes duplicate themselves as nature intended. But colchicine seems to kill the fibers necessary for cell division to occur.

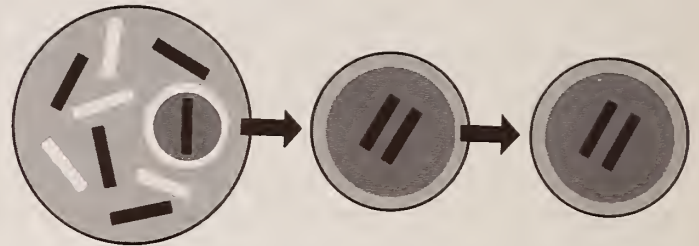


FIGURE 4.—Cells can't divide, so doubling continues until single chromosomes from each pair “organize” a new half cell. They duplicate back to normal, but treated plant is changed forever.

A conclusive test of the chromosome substitution proposal is now underway. Seedlings homozygous for interchanges between chromosomes were treated with colchicine. If substitution were to occur from one genome to the other, at least some mutants would be expected to have four identical structurally marked chromosomes.

Replacing the Original Growing Point After Treatment

Since tetraploid nuclei have approximately twice the volume of diploid cells, it was considered that the results of a reduction division should be detectable after treatment of tetraploid seedlings (5). It was found that diploid cells were present in the region of the growing point as early as 2 days after colchicine application, and that diploid cells divided to form a new apical dome replacing the tetraploid cells and forming a whole new growing point. By the 5th to 9th day after application of colchicine, the apical domes in some instances were made up wholly of diploid cells. Thirteen formerly tetraploid seedlings had diploid cells in the region of the growing point among a total of 75 tetraploid seedlings which were sectioned and examined at 13 daily intervals after colchicine application.

Among treated seedlings, which were not sacrificed for study, were 2 diploids of 4 survivors out of 40 treated plants. Of the untreated seedlings used as controls, 15 were sectioned and found to contain no diploid cells. In addition 56 were grown to maturity and no diploid plants were found. Nuclear changes were also observed in diploid seedlings of Experimental 3 and Norghum after colchicine treatment (30). The mean nuclear volumes were measured in the apical dome region of treated seedlings fixed and sectioned as above at daily intervals after application. An initial increase in volume was noted and a first maximum was reached at the 3d to 5th day. A decrease then occurred until by the 8th or 9th day the original diploid nuclear volume was observed. A further increase in volume was noted up to the 13th day at which time the study was carried no further. It would appear that a diploid or partly diploid apical dome was formed after the initial increase in nuclear volume. Ploidy again increased as these cells were acted on by the residual colchicine.

These studies have illustrated how a growing point could be transformed into a different genotype than the original. Chimeras of polyploid and normal tissue are commonly found after colchicine

treatment of growing points of many plant species. Likewise in some instances the presence of chimeras of the original and the mutant genotype have occurred. This has been inferred since progenies of treated plants have been found which included plants of the original genotype in addition to mutated plants (35). In these instances the whole apical dome must not have been replaced by the mutated cells.

Mechanism of Somatic Chromosome Reduction After Colchicine Treatment

The manner in which somatic reduction of the chromosomes may occur is difficult to study, since evidence can be obtained only by inference. Because of the unfailing formation of 10 chromosome pairs at prophase of meiosis in the mutants, a completely functional complement of chromosomes must result from the reduction process. This is further corroborated by the separation of members of at least 4 of the 10 chromosome pairs which were structurally marked to demonstrate reduction (36). Since chromosome relationships in the haploid mutant did not differ from those in a haploid of the original genotype, an exact haploid set of chromosomes appears to be represented in the haploid mutant. To achieve this exact complement, either a mechanism was present effecting a precise separation of members of each pair, or a selection process took place capable of selecting a balanced chromosome complement from among the numerous combinations that might occur by chance. There is also the possibility that repulsion force may tend to separate haploid sets which are afterwards selected over aneuploid aggregations.

Within colchicine-treated coleoptiles of sorghum seedlings, multinucleate cells are commonly seen in the neighborhood of the apical dome. An apparent phragmoplast formation between nuclei within such a cell was noted (4). It is proposed that a cell formed by somatic reduction of the chromosomes in a multinucleate cell may divide to form a new tissue. During the early period of investigation of the effects of colchicine, the paraffin section technique was used and the formation of phragmoplasts within multinucleate cells described in at least three separate studies (3, 24, 25). Cells containing only one nucleus originated as a result of the formation of cell walls which cut off solitary nuclei from

multinucleate cells.

The question of whether some force causes a group of chromosomes representing a balanced chromosome complement to form a nucleus in a multinucleate cell could not be answered in sorghum, since individual chromosomes cannot be identified. Gläss (17), however, has shown how a complete genome may separate from the rest of the chromosomes in a tetraploid cell of the rat. Recently Knight *et al.* (23) have noted root-tip cells in *Ribes* with chromosome numbers from 8 to 24, including 3 cells having the diploid number of 16 after treatment with para fluorophenylalanine. In untreated material no reduced cells were found. This treatment, however, gave no abnormal shoots.

A possible explanation for the appearance of the homozygosity noted in the mutants has been proposed by Nielson and Drolsum (28). On the basis of their measurements of nuclei in untreated root tips of Experimental 3 they considered that variations from the diploid occurred. This was substantiated to their satisfaction by examination of squash preparations of root tips in which they found variations from the diploid chromosome number. From this they presumed that a haploid cell might occur as a result of the unbalance between the cytoplasm and nucleus caused by the differences between the original parents of the hybrid. Such a haploid cell occurring before treatment could then be doubled by the action of the colchicine to form a homozygous diploid cell. Nuclear measurements made in apical dome paraffin sections of Experimental 3 have not confirmed the observations made on the instability of the cellular makeup of this variety. No difference could be discerned in variability of nuclear volume between Experimental 3 and Norghum. On the basis of what is known at present it seems more likely that the explanation for the origin of the haploid cells may lay in the cutting off of nuclei from giant multinucleate cells formed as a result of colchicine action as described by earlier workers and noted recently by Chen and Ross (4).

Factors Effecting Induction of Somatic Reduction

Though colchicine has been used as a polyploidizing agent in plant work by many investigators for almost thirty years, results similar to those described in sorghum have been noted only rarely. Recently, however, mutational effects (including homozygous

mutations) after colchicine treatment of barley seedlings with colchicine-lanolin have been reported by workers at Purdue University (16). To establish the cause for the differences in effect of colchicine, conditions have been examined under which mutants occur after colchicine treatment. It was shown that differences between genotypes could be responsible for differential reaction to colchicine (1). Experimental 3 gave 24 diploid mutants and no tetraploids out of 43 survivors while Norghum, a released variety, gave 4 diploid mutants and 5 tetraploids out of 54 survivors. Exceedingly favorable conditions after colchicine treatment were not found conducive to the appearance of mutants (34). Light quality appeared to be important in determining the appearance of the phenomenon in a study made by Franzke *et al.* (15). Unpublished work has demonstrated, however, that other components are also important since even with control of temperature, light, and all other factors heretofore considered necessary, mutants have not been produced in recent experiments. One factor under consideration is the possibility of differences in the colchicine lots since it is not a synthesized product. Continued research is underway to more clearly define the necessary conditions.

Implications of Somatic Reduction Regarding Uncontrolled Growth

The demonstration that somatic chromosome reduction may occur after colchicine treatment suggests that it may also obtain under naturally occurring stress conditions. These may include locally abnormal concentrations of metabolic by-products or hormones. Externally inflicted stresses whose effects may result in the former may also have a direct effect upon cellular metabolism. If a reduction of the chromosomes followed by doubling were to occur in conjunction with mutagenic effects, a mechanism that would give drastic change in cellular potential would be readily at hand. This has implications from the standpoint of uncontrolled growth (29) as well as the controlled growth in which context the somatic reduction divisions have been studied in sorghum. In cells in the region of the apical dome, a hormonal balance may be achieved which would not be expected within animal tissues since no localized growing points are present. Carcinogenesis might occur as a result of

a mutational effect with or without somatic reduction. The nontrue-breeding sorghum mutants showed a great deal of heterosis which under certain conditions outside of hormonal control could have its counterpart in cells exhibiting only uncontrolled growth. Selective forces must be present within the meristematic region of the sorghum seedling, which would prevent the proliferation of a cell not having the totipotency to form an entire plant. Uncontrolled growth also could result from the absence of a proper hormone balance within the particular tissue. Conditions determining morphogenesis and development are still improperly understood.

Use in Plant Breeding

In sorghum, somatic chromosome reduction and its concurrent mutational effect when induced after colchicine treatment, have been used with success in the breeding program at South Dakota State University by Professor C. J. Franzke. Many valuable mutants have been obtained which have added to the genetic variation from which selection for adapted types might be made. The selection process has been facilitated, since true-breeding types immediately obtained after treatment can be placed in adaptation trials directly without the painstaking work of selection over a number of generations. Winner, a white-seeded, early maturing variety was obtained as an immediate mutant after treating a seedling of Experimental 3. Dual, a forage or grain type sorghum variety, was obtained after colchicine treatment of a hybrid seedling from a series of complex crosses. This variety has been used as the fertility restorer line in the forage and grain hybrid 252F. SD 100 and SD 102 used in the hybrids 502, 503, 441, and 451 as fertility restorer lines have been obtained as immediately true breeding lines after a series of colchicine treatments combined with selection and crossing.

Barabás (2) in Hungary studied the effects of irradiation with X-rays and colchicine on a strain of sorghum. He concluded that colchicine could be used with greater efficiency than X-rays to produce extreme forms with breeding value. Haensel *et al.* (18) had previously come to a similar conclusion.

Gilbert and Patterson (16) reported the induction of colchicine mutants in a winter variety of barley, Decatur. They employed the same method of treatment as that used by the South Dakota work-



ers and essentially the same type of results was found as observed in the sorghum variety Experimental 3. Some of the treated plants were immediately homozygous for the changed characters while others were heterozygous. In addition, similar or identical mutants were found, and in some of these, changes appeared to be of agronomic importance, particularly mildew resistant mutations.

Summary and Conclusion

Somatic chromosome reduction has been found to occur naturally under specific circumstances in certain organisms. The induction of this phenomenon was inferred on the basis of genetic evidence after colchicine treatment of sorghum seedlings of certain varieties. Some of the treated seedlings were changed immediately into diploid mutants, a proportion of which bred true immediately for the changed characteristics. It was proposed that the true breeding nature of these mutants resulted from a somatic chromosome reduction followed by dou-

bling to restore the diploid number. Confirmation of this proposal was made when it was found possible to induce diploids from tetraploids, a haploid from a diploid, as well as separation of marked chromosomes distinguishing members of pairs. Seedlings heterozygous for interchanges between chromosomes were treated with colchicine. Mutants were produced and found to be homozygous for the marked chromosomes both in instances where 2 pairs were marked and where 4 out of the 10 pairs were marked. On the basis of the above evidence it would seem that the whole chromosome complement underwent a reduction division which was normally followed by doubling to restore the diploid number.

To explain the mutational effect it was postulated that *Sorghum vulgare* is an allopolyploid made up of 5 chromosome pairs from each of two ancestors. An imperfect reductional division which allowed a concentration of chromatin from one of the ancestors would be expected to give a changed plant.

This hypothesis was supported when it was noted that mutants appeared to fall into certain classes and that identical mutant genotypes occurred. Many different genes were found to be changed within one mutant and these were inherited in a Mendelian fashion. On the other hand, no cytogenetic evidence for duplication of chromatin or chromosomes was noted. Meiotic behavior of the mutants and their F_1 hybrids with the original genotype was normal. Ten bivalents were always found in these materials as well as in the original genotype. Mutated genes were found to be inherited independently. Substitution of chromosomes from one genome to the other would give consistently at least one bivalent at prophase of meiosis in an induced haploid mutant. This expected bivalent formation did not occur. This evidence more than any other, would seem to favor the theory of gene mutations rather than chromosome substitution as an explanation for the changes in genotype.

In studies of the growing point of colchicine treated tetraploid sorghum seedlings, the replacement was noted of polyploid cells in the apical dome region by diploid cells. It appeared that this happened in some instances at the 5th to 6th day after application of colchicine. After treatment of diploid seedlings, initial polyploidization of cells in the apical dome region was followed by formation of diploid apical domes. It was proposed that the diploid cells might in some instances have arisen from a cell originating by somatic reduction, followed by doubling to restore the diploid number.

Chromosome reduction in somatic tissue after colchicine treatment may possibly occur as follows. Within the region of the apical dome of the treated seedling, a polyploid multinucleate cell forms as a result of the action of colchicine on spindle function. A mononucleate cell is cut off from this giant cell by formation of a cell wall. This mononucleate cell could contain a complete chromosome complement and be haploid or homozygous diploid either by chance or through a chromosome segregation force, perhaps favoring separation of homologues.

Many factors affect the occurrence of diploid mutants after colchicine treatment. Among these are genotype of the material, temperature and light conditions after treatment and also, it would appear, changes in the colchicine-lanolin ointment. Recent difficulties in reproducing results from mutation experiments suggest that factors necessary to induce colchicine mutations are not understood, and that more work is needed to elucidate techniques to assure the appearance of mutants.

The use of this phenomenon in plant breeding has been demonstrated in sorghum. A number of released varieties and inbred lines used in commercial hybrids have originated by the use of this method. In barley, valuable diploid mutants which were immediately homozygous after treatment have been observed. When conditions determining the occurrence of this phenomenon have been defined, it has promise as an important tool in increasing the ease with which crop plants can be moulded for the use of man.

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Pathways and Mechanisms for

Foliar Absorption of Mineral Nutrients

W. H. Jyung, S. H. Wittwer



The importance of the green leaf as the primary site for photosynthesis in higher plants has overshadowed a lesser but potentially important function of plant foliage. Absorption of surface applied solutes, though secondary, is daily assuming a greater significance. The most effective use of mineral nutrients, herbicides, antibiotics, growth regulators, systemic insecticides and fungicides, is contingent upon a knowledge of the mechanisms of uptake by leaf surfaces.

Most mineral nutrients applied to aerial plant surfaces are readily absorbed and translocated to all plant parts. The mechanisms of uptake and pathways of entry, however, have not been fully resolved. Present concepts are limited, controversial, and provide only fragmentary information.

Most investigations till now have dealt with the sequential pathways of the penetration of foliar-applied nutrients from the leaf surface to the protoplasm within the living cell. Leaf surface morphology has been a primary consideration. Pertinent information thereto will be assembled and

presented in light of latest developments within our laboratories and elsewhere.

Mechanisms of nutrient absorption by leaves may vary with substances applied and the plant species being examined. Fundamental enzyme kinetics provide some intuitive insight into mechanisms of ion uptake by leaves, as do the accumulating evidences for a coupling between nutrient uptake and cellular metabolism.

PATHWAYS OF PENETRATING NUTRIENTS

Stomata

As possible portals of entry for foliar-applied chemicals, stomata were among the first to receive attention. Conflicting evidence has been presented as to their role in nutrient uptake through leaf surfaces. Many reports show apparent correlations between the number of stomata per unit leaf area and rates of absorption. In other cases, however, no correlation has been found between the frequency of stomata and the quantity of nutrient absorbed. Occasionally, more absorption has been recorded through upper leaf surfaces which have no stomata or only a small percentage of the stomata found in the lower leaf surface.

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Recent advances in the chemical control of the closing of stomata have encouraged additional studies on their role in ion uptake (16).¹ Results indicate that foliar absorption of rubidium (Rb) was more a function of stomatal frequency and leaf thickness than of stomatal opening.

Suberization of the air-exposed surfaces of mesophyll cells within stomatal cavities results in an internal cuticle. Thus, stomatal entry by solutes is not equivalent to absorption. The penetrated materials may be considered within the leaf but not in the cells. The necessity for penetration through a layer resembling cutin or suberin (31) still remains.

Ectodesmata occur in great profusion in and around stomatal guard cells (9), and may serve as important pathways for penetrating nutrients. Cuticles on the lower surfaces of leaves are generally thinner than those on the upper surfaces. Furthermore, in many species, stomata are present with greater frequency or occur only on lower leaf surfaces.

Stomatal cavities, if penetrated by spray solutions, greatly increase the potential absorbing surface of the leaf. They also present a cuticular surface which is thinner, more hydrated, and permeable than that covering the outer leaf surface. These findings focus attention on the presence of stomata as they modify, or may be related to the ease of cuticular penetration of substances applied to leaf surfaces, rather than as portals of entry *per se* into the leaf cells.

Cuticle

Cuticular penetration has been repeatedly emphasized by those who have found no apparent correlation between the stomatal frequency and the degree of nutrient uptake. From the foregoing discussion that stomatal entry does not preclude the necessity for cuticular penetration, there is no alternative but that the initial barrier for foliar absorption is the cuticular membrane. Thus, the cuticle is the main, if not the exclusive, route of entry. Passage of nutrients through cracks and other imperfections has been designated as intercuticular penetration (39).

Recent studies of nutrient permeation through isolated cuticular layers have contributed greatly

to an understanding of foliar absorption. Penetration through cuticles has been commonly assumed a physical diffusion process. Convincing evidence, however, awaited the thesis of Yamada (40). With astomatous cuticles of ripe tomato fruits and the stomatous cuticles from green onion leaves, he demonstrated that ion penetration followed a typical diffusion equation. Absence of respiratory activity in these membranes is presented as supporting evidence. Permeability of cuticular membranes to isotopically-labeled cations (Ca^{45} , Fe^{59}) was greater than that for anions (P^{32} , S^{35}). Inorganic ions penetrated more rapidly from the "outer" side to the "inner" side (influx) than from the "inner" to the "outer" side (efflux) of cuticular membranes which were enzymically isolated from tomato fruit and green onion leaves (41). The greater ion binding capacity of the "inner" surface was proposed as the explanation (42). This rationale, however, does not account for the exceedingly high permeability of urea (44). Penetration rates exceeded by 10 to 20-fold those for cations and anions. Binding of urea on cuticular surfaces was only equal to or much less than that for cations, and was the same on outer and inner surfaces of both types of cuticles.

Goodman and Addy (10) reported the reverse results for penetration of C^{14} labeled urea, benzoic acid, glucose, maleic hydrazide, and simazine through chemically-excised apple leaf cuticles. Penetration rates were not appreciably greater than for an inorganic cation, and movement from the inner (mesophyll) surface to the outer (air) surface exceeded that from the outer to the inner surface. Our data show that the influx and the efflux of urea through the stomatous cuticular membrane isolated enzymically from green onion leaves were approximately equal (44). Furthermore, it is suggested that cuticular penetration of urea was not governed by first order kinetics, and was something other than simple diffusion. Perhaps a "facilitated diffusion", resulting from a change in the structure of the cuticle itself, may account for the higher rate of urea penetration than that of ions.

Time course studies have revealed that not only does urea penetrate cuticular membranes at a remarkable rate (10 to 20-fold greater than nutrient ions) but this rate increased with time (44). Furthermore, urea increases the rate of foliar uptake of

¹ Italic numbers in parentheses refer to Literature Cited p. 35.

other nutrients which may be added simultaneously. Facilitation of absorption occurs at the cuticular level for anions, and at both the cuticular and cellular levels (see below) for cations (43). This unique characteristic of foliar-applied urea which itself is a proven source of nitrogen for many crop plants (38) may account for its now recognized beneficial effects as an ingredient in diverse types of nutrient sprays (43).

Crafts and Foy (5) have suggested that within the cuticle there are at least two routes for penetration of applied materials into plant leaves, a polar or aqueous route, and a non-polar or lipoidal route. Cuticles are thus permeable to both polar ions and non-polar fat soluble substances.

Most investigators have assumed that upon isolation, cuticular membranes maintain their integrity and natural permeability characteristics. However, the rate of penetration of substances through isolated cuticular membranes is much slower than when they are intact on the leaf surface (10). Goodman and Addy have further emphasized that changes occur during the chemical isolation of cuticles, and this is likely true for enzymic separation also. Comparative evaluations of permeabilities of cuticular membranes derived by chemical, enzymic and mechanical separations have not been conducted.

In conclusion, molecular size, charge, partition, volatility, solubility, and adsorbability (sorption) are important in solute penetration of cuticular membranes. Recent studies suggest that partition and solubility may play a dominant role in cuticular penetration of urea and maleic hydrazide, while molecular size, charge, and adsorbability are relatively important for inorganic ions (41, 42, 44).

Ion Uptake by Isolated Leaf Cells

Once the cuticular entry of nutrients is accomplished, they may be either absorbed directly by leaf cells or diffuse within a free space volume. Ion uptake studies by isolated leaf cells of various types (spongy, mesophyll, palisade, epidermal, guard cells) may be one of the most useful approaches for the future in resolving mechanisms of foliar absorption (17). Living cells removed from leaf tissues and suspended in solution offer a system for physiological studies far better defined than is possible for the intact leaf. The

structural and functional heterogeneity typical of intact leaves is considerably reduced. All concern for differences associated with stomatal vs. cuticular penetration as well as for bona fide movement of ions through cracks on leaf surfaces is eliminated. Absorption studies in the absence of translocation become a reality. Furthermore, the effects of various metabolic processes (photosynthesis, respiration) on ion uptake become subject to easy manipulation. Heretofore, it has been assumed that absorption pathways and mechanisms as revealed by intact or excised organs and slices of storage tissues reflect those of plant cells (13). Results of ion uptake studies thus far conducted with isolated leaf cells suggest that the coupling between absorption and metabolism occurs at the cellular level during the overall course of foliar absorption of mineral nutrients (17).

Cell Wall

A cell wall of variable thickness, depending upon the presence or absence of ectodesmata, has to be traversed by penetrating nutrients before contact with living protoplasm is effected. In general, cell walls have a high cation exchange capacity. They are further considered as a part of plant tissue that is in equilibrium with the external environment. This has been designated as the apparent free space (AFS). According to Laties (21) AFS consists of both water free space (WFS) where solutes enter by free diffusion and Donnan free space (DFS) where there is cation exchange according to Donnan equilibrium. Thus physical diffusion has been presumed as the mode of cell wall penetration although direct proof is lacking.

The diffusion phenomenon of cell wall entry has received support from those who have favored the AFS concept. The presence of an AFS has been demonstrated in leaves as well as in roots. Levitt (22) showed that the values of AFS for plant roots corrected for surface film approached two-thirds of the cell wall volume. Cell walls are now generally considered as a part of the free space volume though no critical evaluation of it has ever appeared. If cell walls are a part of AFS, there must be free and rapid "tangential" transport of ions along all walls. This is most unlikely as has been pointed out by Arisz (1). Otherwise, potassium cyanide applied to the mid-zone of a leaf would translocate by means



of the cell walls and affect absorption far beyond the site of treatment. This was not observed. Accordingly, Arisz concluded that "a wall transport not controlled by the cytoplasm is not present in *Valisneria*." The significance of ion binding to cell walls, however, cannot be overemphasized. These bound ions could later be actively taken up by protoplasmic particulates. Evidence is also accumulating that cell walls are not entirely metabolically inert, but may participate in the active uptake of solutes. Enzymes, other proteins, and ribonucleic acid (RNA) have been identified in the cell walls of higher plants.

Ectodesmata

Plasmodesmata-like strands occur in the outer cell walls of leaves. They often extend through the epidermal cell walls up to and just beneath the cuticle. Franke (9) has designated these strands as ectodesmata and concluded that they provide pathways for transport of substances in and out of leaves. This view has been subsequently supported by others. The likely role of ectodesmata in foliar

absorption has also, as mentioned earlier, helped to resolve many questions associated with stomatal and cuticular penetration.

Plasma and Vacuolar Membranes

Classically, the plasma membrane is designated as a semi-permeable (layer) immediately beneath the cell wall and enclosing the cytoplasm. Direct electron microscopic observations have verified its existence. Passage through this membrane is prerequisite to a full utilization of foliar-applied nutrients.

Many factors affect the permeability of this membrane. Mechanisms peculiar to plasma membrane penetration in plant cells have been reviewed in terms of differences in electro-chemical potential (6). Whether the electro-chemical potential is the result or cause of active transport has not been resolved. Dainty (6) concluded that the Na pump (a hypothetical active transport mechanism) is located in the plasma membrane, whereas that for Cl is in the vacuolar membrane (tonoplast). Recently, Saltman *et al.* (30) affirmed that the outwardly-directed Na pump is located in the plasma membrane. They suggested that K could enter the cell either by passive diffusion as a counter ion or by an inwardly directed exchange mechanism coupled to the Na pump. Chloroplast membranes were also semi-permeable, and the expected Na pump was there likewise.

Lundegardh (23) has theorized that anion accumulation is coupled to the cytochrome system in respiration, and anion transport is along a potential gradient dependent on the outward transfer of electrons. Similarly, Robertson (29) proposed that an initial separation of positive and negative charges through the electron transport chain was necessary across a unit membrane that was only slightly permeable to ions of the same sign. This was accomplished by the outward movement of electrons, and provided a model for an anion-permeable membrane as a result of charge separation. His model ignored the presumed obligatory requirement for adenosine triphosphate (ATP). This cannot be reconciled with evidence that salt uptake is coupled with an ATP generating process. These models do not explain the specificity of ion uptake and inhibitory effects of 2,4-dinitrophenol (DNP). Robertson's scheme has been recently modified and

an anion-carrier model proposed (3). The carrier is oxidized at the external surface and reduced at the inner membrane by an electron. Consequently, anion movement, after combining with the appropriate carrier, is along a concentration gradient, whereas cations pass through negatively-charged pores.

Endoplasmic Reticulum

The startling concept that plant cells may consist of a three dimensional system of membrane-bound cavities in a finely granular matrix is indicated by studies of the endoplasmic reticulum (25). This reticulum may form a continuous network permeating the entire cytoplasm from the plasma membrane, through mitochondria, the nucleus, and even to the tonoplast surrounded vacuole. The unit membrane description is that all membranes in the cell are topologically continuous either permanently or during genesis. Future problems and approaches relative to active transport and permeability may develop a new focus. Of particular significance is that endoplasmic reticulum-like membranes have been induced from the ground substance of cytoplasm within seconds by stimuli that generally exert a profound effect upon active transport of ions (37).

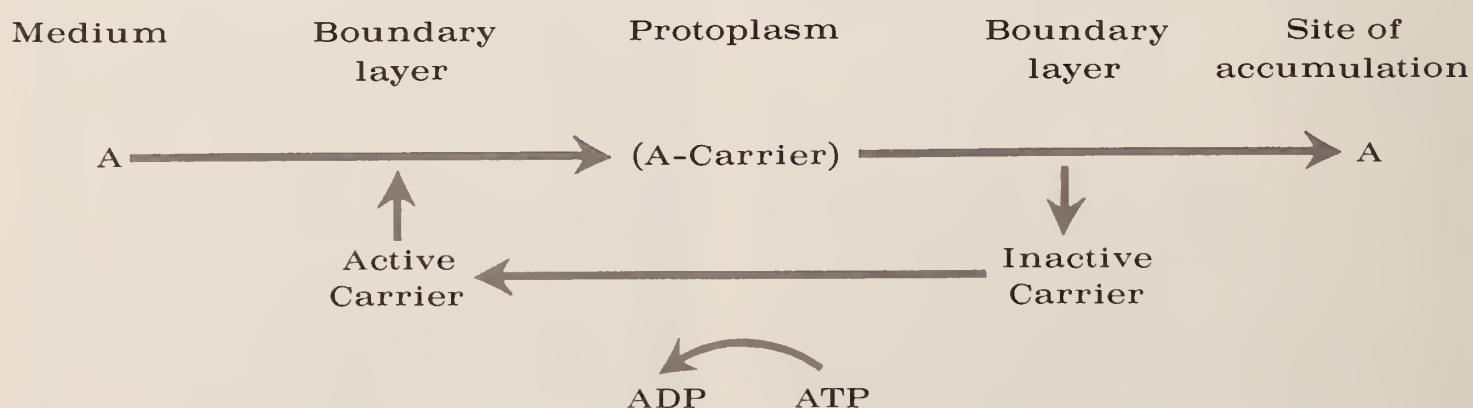
CARRIERS

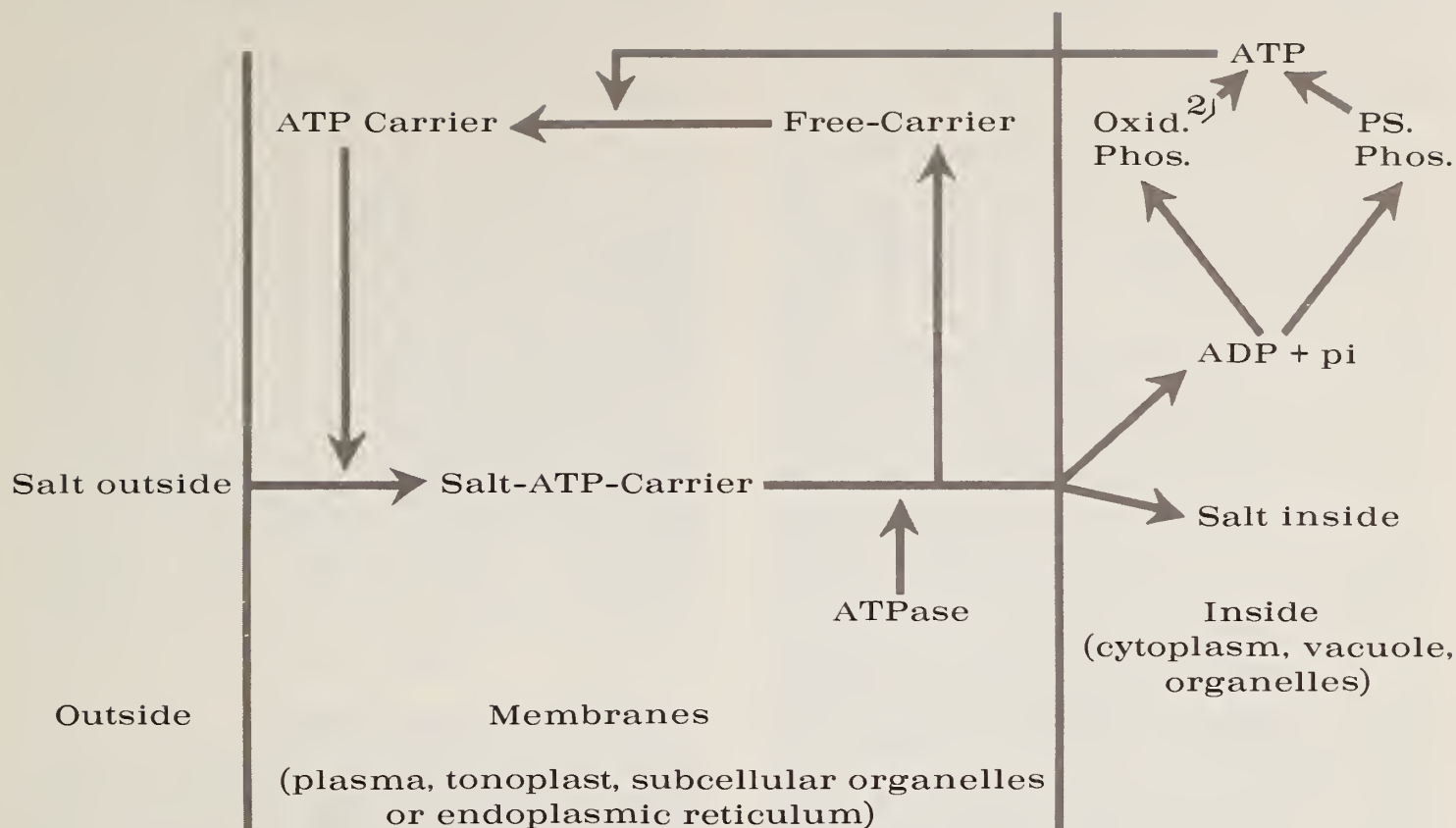
The carrier concept as an approach to active uptake has gained in popularity during recent years because it accounts for the specificity of nutrient uptake. The proposed carrier functions as follows. The ion combines with metabolically-produced binding compounds at the outer surface of a membrane which is impermeable to free ions. The carrier-ion complex reaches the inner surface where a

chemical change coupled with metabolism occurs in the binding compound or carrier to set the ions free. Carriers may be present in membranes and the cytoplasm. Energy is presumably required either for their formation or maintenance, or for both. The isolation and identification of carrier(s), however, has not been accomplished. This is needed for an objective biochemical analysis of active uptake processes. The following have been suggested as possible carriers of active sites in plant and animal cells, yeast, and bacteria: phosphoprotein, pyridoxal, phosphatidic acid, N-terminal histidine, steroids, mannampotein, adenosine triphosphatase (ATPase), phosphoryl choline, RNA, and ribonucleoprotein.

It is generally assumed that carriers are proteinaceous. This view is supported by reports describing the inhibition of ion uptake by D-chloramphenicol, which is a specific inhibitor of protein synthesis in bacterial systems. This presumption is further supported by the results of current studies on ion uptake and protein synthesis in enzymically-isolated leaf cells (18). Inhibition of Rb⁸⁶ uptake by the D- and L- threoisomers of chloramphenicol was 83 and 64 percent, respectively. The corresponding reduction in glycine C¹⁴ incorporation into protein was 71 and 48 percent. This parallel inhibition by the D- and L- chloramphenicol isomers on Rb uptake on the one hand, and glycine incorporation into protein on the other, suggests that absorption of Rb by leaf cells is highly correlated with protein synthesis.

A carrier concept appears the most likely for explaining nutrient uptake by green leaves. Since ATP provides the biochemical energy utilized in active uptake processes, Mothes and Engelbrecht (27) proposed the following:





²⁾Oxid. phos. = oxidative phosphorylation; PS. phos. = photosynthetic phosphorylation; ADP = Adenosine diphosphate; pi = inorganic phosphate.

ATP activates the carrier. The substance-carrier complex (A-carrier) moves through the outer boundary (plasma membrane) to the cytoplasm and then through the inner boundary layer to an accumulating site (vacuole, mitochondrion, plastid). There is evidence that ATPase is present in plant and bacterial cell walls and membranes of animal cells. ATPase activity is also suggestive of active transport. The scheme above is proposed for active ion uptake by leaves.

The ATP-Carrier complex may have a stereo-specific conformation comparable to the "permeases" proposed by Cohen and Monod (4). Formation of Salt-ATP-Carrier complex may proceed rapidly. Preliminary experiments have shown that ATP-dependent Rb binding on the cell walls of corn coleoptile was completed within 30 seconds. ATP also increased Rb binding by 30 to 95 percent.

Metal Chelates

Studies of active transport of chelated metals offer a possible approach to the nature of carrier action. A great void exists in our present knowledge of the

foliar absorption of chelated metals. Generally they have not been as successful in correction of nutritional disorders by sprays as have the inorganic salts. Some leading results, however, have been obtained in our laboratory with absorption by intact leaves, permeation of cuticular membranes, and uptake by isolated leaf cells (19). The use of Fe^{59} labeled ethylenediaminetetraacetic acid (EDTA) and ethylenediamine di-o-hydroxyphenylacetic acid (EDDHA) and $\text{Fe}^{59}\text{SO}_4$ has revealed that the absorption of Fe^{59} both by intact bean leaves and leaf cells was greatly retarded by chelation. Transport of the absorbed iron by the leaves of the intact plant, however, was greatly facilitated by both EDTA and EDDHA. Chelated iron penetrated some cuticular membranes more readily than the inorganic sulfate.

CRITERIA FOR ACTIVE FOLIAR ABSORPTION

Evidence for a possible coupling between foliar absorption of mineral nutrients and plant metabolism was first summarized by Wittwer and Teubner (39). Further verification has been achieved

in recent studies in our laboratories (15, 17, 18, 38) and those of Smith and Epstein (32, 33).

Time Course Analysis

Two-phase time course curves in foliar absorption have been reported. Mechanisms peculiar to these phases in root absorption have been outlined by Laties (21). The initial rapid uptake is ascribed to nonmetabolic processes. The slower and usually linear second phase is a function of metabolic control. In many instances, however, the acute break in the time curve for foliar absorption, which presumably represents the transitory phase between the two coincides with the drying, concentration, and crystallization of the solution applied to foliage. Absorption and transport were very rapid until crystallization occurred or as long as the leaves were kept immersed in solution. Thus, the initially rapid absorption of foliar-applied materials may not be peculiarly indicative of nonmetabolic uptake. A linear relationship with time, however, is highly suggestive of a metabolically controlled absorption. Verification must come from an examination of other criteria of metabolic uptake.

Temperature Dependence

Temperature coefficients (Q_{10}) have become perhaps the most classical of all indices for separating active and passive processes within the plant. For chemical reactions, where an Arrhenius temperature dependence holds, these range from 2 to 3. Q_{10} values for foliar absorption—some greater than 2, some less than 2—have been found. Many enzyme catalyzed reactions have Q_{10} values less than 2; some are as low as 1.15. Evidence for temperature dependence suggests that the overall foliar absorption of mineral nutrients is an active process, but Q_{10} values alone are insufficiently definitive.

Energy Dependence

Ion uptake by leaves, if an active process, would be energy dependent. Light is closely associated with the metabolic activity of all living plant protoplasm, and light dependence may be the most indicative of all criteria for an appraisal of energy requirement.

Light, with few exceptions, has consistently enhanced nutrient uptake. In a typical case Kylin (20) compared the effects of light on ion uptake

with green and albino leaves. Light was functional only with green leaves.

Two explanations of the light effect have been proposed. One is the direct influence of light on the permeability of the plasma membrane. The other is that light affects an energy-consuming mechanism for salt uptake associated with photosynthesis. The latter concept has been experimentally substantiated. Convincing evidence is the similarity in the action spectrum for chloride uptake by *Vallisneria* leaves and that for photosynthesis (34).

Results with externally applied energy-rich compounds (sugars, ATP) have been inconclusive. As might be expected, only when internal reserves become limiting does an external dosage prove beneficial (27). Light dependence, which implies an energy requirement, can serve as a critical criterion for metabolic absorption of nutrients by leaves.

Sensitivity to Metabolic Inhibitors

Specific metabolic inhibitors provide a means of ascertaining if foliar absorption of a specific nutrient is likely linked with corresponding metabolic processes. Among commonly used inhibitors, in ion uptake studies is dinitrophenol (DNP), an uncoupling agent in oxidative phosphorylation. Arsenate and iodoacetate inhibit substrate level phosphorylation. Cyanide and azide are oxidation inhibitors and block respiration in coupled as well as uncoupled systems. Gramicidine is an inhibitor of oxidative phosphorylation. Fluoride, phloridzine and cardiac glycosides inhibit the activities of enolase, muscle phosphorylase, and ATPase, respectively. Chloramphenicol and 5-fluorouracil are inhibitors of protein and RNA syntheses.

Some metabolic inhibitors may affect the viscosity of cellular protoplasm. This may physically modify foliar uptake processes independent of metabolic influences.

Irreversible Accumulation Against a Concentration Gradient

This requires expenditure of metabolically-derived energy and is a criterion for active foliar absorption. However, accumulation against a concentration gradient is not evidence for active transport if it occurs along an electro-chemical potential gradient (6).

Irreversible accumulation does not occur as a

consequence of diffusion and exchange processes. This phenomenon (15) is evidence for an active mechanism in ion uptake by plant foliage.

Oxygen Dependence

A process that requires oxygen is usually coupled with metabolic activity. While oxygen dependence is a reality for foliar absorption (15) the requirements may be appreciably less than that estimated for root absorption. Illuminated and photosynthetically-active green leaves may utilize internal oxygen by choice, and its concentration may be even greater than the external. Hence, oxygen dependence for foliar absorption of minerals in the light is a reality but not easily subject to an objective evaluation.

Specificity and Ion Competition

The explanation for specificity of uptake and ion competition resides in metabolically-produced specific carriers. These phenomena suggest an active mechanism for ion uptake. Ion competition studies have not been attempted in the realm of foliar absorption. They could be conducted with ease, however, by utilizing enzyme kinetics as adopted by Epstein and Hagen (7).

pH Dependence

Most enzyme-catalyzed processes are pH-dependent. Foliar absorption is in this category. Analysis of pH effects provides information as to the structure of the so-called "active center" of an enzyme, and is, therefore, a bridge between kinetics and mechanisms. If it is assumed that the specific ion carrier is enzymic, studies of pH-with the proper interpretations, should be of great importance in resolving mechanisms of foliar absorption. Van Overbeek (35) has suggested the pH effect from penetrating chemicals is on plant protein rather than on the substances applied. The degree of dissociation of certain molecules does not usually parallel the pH profile of the penetration rate of that chemical.

Other explanations have been rendered as to pH effects on foliar absorption. Volk and McAuliffe (36) suggested that NaOH increased the permeability of the cuticle. Orgell (28) has indicated that at a pH lower than 5 the cuticle has no charge, while at a pH above 7 the cuticle is negatively charged.

Yamada (40) recorded an apparent pK value of 2.8 for cuticles from green onion leaves, and 3.2 for those from ripe tomato fruits. Thus, pH-regulated electrostatic repulsion and attraction phenomena affect cuticular sorption, and consequently the rate of foliar uptake of ions.

ENERGETICS OF FOLIAR ABSORPTION

There is convincing evidence that the overall process of ion uptake by leaves (15) and specifically ion uptake by isolated leaf cells (17) is coupled with plant metabolism, and the energy utilized in the metabolic transport of nutrients is probably derived from ATP. An ATP requirement has been designated for many processes in animal systems, but little is known for those of higher plants. One example has been reported (24) in which the inhibitory effects of DNP on Rb uptake by excised barley roots were negated by exogenous applications of ATP. This influence was non-specific, however, because both adenosine diphosphate (ADP) and adenosine monophosphate (AMP) were likewise effective.

Two major energy (ATP) supplying processes for possible enhancement of active ion uptake by plants are oxidative phosphorylation in mitochondria and photosynthetic phosphorylation in chloroplasts. The former has been demonstrated with oxygen tension as a variable, and by observing the effects of specific metabolic inhibitors such as DNP, KCN, and NaN_3 . The latter has been suggested by evidence derived from light-dark experiments, those with green and albino leaves, the similarities in action spectra for ion uptake and photosynthesis, and the promotive effects of externally applied sugars.

Energy (ATP) may be utilized for (a) the synthesis of carriers, (b) the required molecular rearrangement of carriers, (c) activation or phosphorylation of carriers, (d) the formation of substance-carrier complexes, or for a combination of any or all of these. One or more of the energy transferring intermediates may be involved in the coupling between ATP and the transport mechanism. No experimental evidence, however, is yet available to support any of these possibilities.

The energy requirement for foliar absorption is subject to many variables. It is probably greater for substances which do not readily penetrate into cytoplasm, such as phosphate and amino acids.



Free energy of activation (ΔF) can be used in estimating the amounts of energy needed.

KINETICS OF FOLIAR ABSORPTION

The carrier concept of active transport, as an analogy of the classical Michaelis-type enzyme kinetics, was first proposed by Epstein and Hagen (7) for resolving the mechanisms of ion uptake by barley roots. Since that time much work has been done on kinetics of nutrient uptake by plant roots. The earlier studies were reviewed by Laties (21). In the meantime a few experiments have been conducted with plant leaves. The absorption systems for phosphate and Rb in bean leaves by means of the apparent K_m and V_{max} have, however, been characterized (14), and the kinetics of potassium

and rubidium absorption by corn leaf tissue reported (33). The high phosphate and Rb absorption values for K_m in bean leaves (14) suggests that the carrier-nutrient affinity is low and a high nutrient concentration is necessary to obtain V_{max} .

Other kinetic characterizations of a particular nutrient absorption system include the determination of the reaction order, the rate constant (k), and time required for the 50 percent absorption ($T_{1/2}$). It has been reported that absorption of phosphate by bean leaves was first order, while that for Rb was a complex of zero and first orders (14). Kinetic data alone are not sufficient for resolving mechanisms of ion uptake. A close fit of absorption with a first order reaction equation merely suggests that uptake may be passive. Other criteria as outlined in this report should also be considered.

COMPARATIVE MECHANISMS IN FOLIAR AND ROOT ABSORPTION

External and internal membrane barriers and cellular mechanisms may be comparable in roots and foliage. Cuticular membranes, though apparently ubiquitous to all external plant surfaces including roots (31), vary greatly in thickness, composition, surface exchange properties, and permeability. The cuticle on leaves presents a more or less formidable barrier to penetrating substances, but may be of little consequence on root hairs. Leaves fix carbon dioxide in the presence of light, and the process of photosynthesis may exert profound influences on ion uptake, the magnitude of which are not presently known. Time course studies and temperature effects on Rb absorption by barley roots (8) have a parallel with those for bean leaves (15). The results of additional comparative studies of absorption based on unit area of exposed surface would be revealing.

PROJECTIONS FOR THE FUTURE

The ultimate goal in resolving mechanisms and identifying pathways for nutrient absorption by plant foliage will be to separate the leaf into its component parts and diverse cell types (spongy, palisade, epidermal, guard), and study permeability characteristics and the rates of ion flux into each. Since cuticular membranes cover all aerial plant

surfaces, foliar uptake must occur through this—the first mechanical barrier to the influx of nutrients.

Considerable progress has already been made in the enzymic separation of the various leaf tissues and many permeability characteristics of the non-cellular cuticular membrane are known. Penetration is by simple diffusion for first order kinetics or, in organic compounds such as urea, a “facilitated” diffusion for higher order kinetics. The physical properties of cuticular surfaces vary greatly. These variances include their ion exchange capacities which have marked effects on directional fluxes of penetrating substances. The remarkable effect of urea at both the cuticular and cellular levels in enhancing its own absorption as well as that of other nutrients is reported. This discovery may have profound implications in the future of foliar feeding.

Relatively pure preparations of leaf cells consisting of a mixture of palisade and spongy mesophyll

have been made. Ion-uptake studies have revealed that absorption at the cellular level within the leaf is coupled with metabolism. Future work lies in a critical evaluation of the carrier concept, and ultimately in the direct isolation of carriers or carrier-like substances. New and fruitful areas for research may also lie in a study of salt uptake by mitochondria, the principal energy-coupling organelles in leaf tissue and by isolated chloroplasts. Recent studies (2, 11, 26, 12) on ion uptake may project a major research effort into this subcellular realm as well as into the role of the endoplasmic reticulum which may provide a continuous network of membrane-bound cavities permeating the entire cytoplasm from the plasma membrane to the nucleus and the vacuole bounded by the tonoplast. Such efforts will eventually center on the biochemistry of ion transport. Only then will mechanisms of active transport, as now revealed by kinetic and thermodynamic approaches, become subject to easy manipulation.

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FORUM

STATISTICS AND RESEARCH

Efficient use of public funds for agricultural research is paramount in assuring optimal returns in information. Such use necessitates the designing of efficient experiments to insure the reliability of experimental inferences and maximum information per dollar spent.

Because of uncontrolled variability in experiments, additional effort and consequently more money are required to adequately measure the effects of experimental treatments and to determine whether differences between treatments are too large to be reasonably ascribable to chance or uncontrolled variation. It is here that statistical methods can play an important role by serving as a tool for the investigator to evaluate the reliability of his results at associated levels of probability.

Proper planning of experiments leads to: (1) Control of bias, (2) maximization of information for a given monetary investment or a given set of laboratory or field facilities, and (3) minimization of monetary investment or laboratory or field facilities to obtain the desired experimental data. Attaining these objectives requires efficiently conducted research and careful planning on the part of the investigator before initiating the experiment.

An investigator should always remember that statistics is only a tool to research and, as with all tools, it must be used with skill, common sense, and judgment to be most effective. As a result of 40

years of experience in active research work, research administration, and now in experimental statistics, it is my judgment that too many experiments are initiated without a well-conceived set of objectives. A researcher once said, "It is likely that some of these debatable points can be adjusted after the tests get underway and that the test will provide certain valuable information." Unfortunately, this situation still is all too common in the conduct of research. The use of appropriate experimental design and corresponding statistical analysis not only insures valid conclusions, but also requires the experimenter to clearly delineate the objectives of his experiment.

The lack of mathematical training, although very important, is not the most serious handicap to the scientist. I am inclined to be equally concerned about the scientist's concepts of the scientific method. Claud Bernard, the eminent French physiologist, said:

"Good methods can teach us to develop and use to better purposes the faculties with which nature has endowed us, while poor methods may prevent us from turning them to good account. Thus, the genius of inventiveness, so precious in the sciences, may be diminished or even smothered by a poor method, while a good method may increase and develop it . . . In the biological sciences, the role of method is even more important than in other sciences because of the complexity of the phenomena and countless sources of error. . . ."

Einstein pointed out in his "Evolution of Physics" that "the formulation of a problem is often more essential than its solution. . . ."

These statements emphasize the need for a thorough evaluation of the research problem and the experimental design before work is initiated. An important aspect of these considerations concerns the basic principles of the scientific method involved in practically all experimentation. To some, the consideration of the scientific method may appear rather obvious, but still too often due consideration is not given to these principles which form the basis for the conduct of efficient and effective research.

I have no desire to persuade a researcher to indulge in an orgy of statistical calculations merely to present an air of statistical respectability to his work.

Far more important than the indiscriminate statistical analysis of every set of experimental data is the cultivation of a statistical habit of mind. With this as a guide, the investigator can judge whether his data require a statistical analysis to aid in interpreting results. If the answer is affirmative, he can determine (a) whether the analysis is of such a standard pattern that he feels competent to perform it himself, or (b) whether he needs the assistance of a statistician.

The proper evaluation of research data requires a knowledge of statistical techniques and their application to research problems. Statistics is as dynamic as the natural and physical sciences. Consequently, the research worker cannot be expected to be highly qualified in both statistics and his own field of research. The alternative is to provide the services of a statistician to help the experimenter in planning his experiments so that the results will effectively and efficiently answer definite questions.

It should be apparent that the close cooperation of the researcher and the statistician is essential for the most efficient expenditure of research funds. The choice seldom lies between using and not using statistics, but between using invalid or inefficient statistical methods and using appropriate specialized techniques.

It is in the areas of choice and experimental design and statistical analysis of data that the statistician can play a significant role. The effectiveness of his efforts, however, are enhanced by a close working relation with the scientist. The part played by the statistician frequently requires considerable forethought and study. This is especially true where the research involves a large number of experimental variables and extends over several years or involves large animals and consequently large expenditure of research funds.

Let us look at a problem that requires both planning and the application of a particular statistical technique to assure feasibility of conducting the experiment as well as being sure of obtaining appropriate data upon which to make proper inferences. This experiment is concerned with canning of sweet corn. The objective is to determine the extent to which both variety and level of moisture at harvest influence the quality of processed sweet corn.

The factors considered in this experiment are 8 varieties, 4 levels of moisture, 4 replications in the field experiment, and subsequently 2 temperatures

of blanching, 2 temperatures of dehydration, 2 temperatures of storage and 2 durations of storage. A complete factorial experiment to study these factors would require 2,048 treatment combinations. By means of a statistical technique called fractional replication, it is possible to use an experimental design requiring only 512 treatment combinations. Thus the amount of work necessary to conduct this experiment has been reduced 75 percent to a size that could be more readily handled.

The fractional factorial experiment obviously cannot produce as much information as the complete factorial experiment. In this situation, economy is achieved at the expense of assuming that certain high-order differential responses (interactions) of some factors in the experiment are negligible or unimportant.

A better understanding of statistical methods by the research worker inevitably leads to a closer working relation and better communication with the statistician. In addition to the broadening of the researcher in statistics at the academic level and the availability of a consulting statistician, there is a need for special in-service training for the subject-matter research specialist. Many present day researchers did not have an academic training in statistics and experimental design. Others did not receive adequate training.

The consulting statistician must accept the responsibility for training researchers who need more background information in experimental statistics. The topics included in in-service courses for scientists must be governed by the requirements of the subject matter to which they are oriented. However, all courses should include the basic principles of statistics and experimental design. It is also important to point out the limitations and applications of the various techniques.

Discussing the responsibility of the consulting statistician, Sir Ronald A. Fisher said:

"The statistician is no longer an alchemist expected to produce gold from any worthless material offered him. He is more like a chemist, capable of assaying how much of value it contains, and capable also of extracting this amount, and no more. In these circumstances, it would be foolish to commend a statistician because his results are precise, or to reprove him because they are not. If he is competent in his craft, the value of the results follows solely from the

value of the material given him. It contains so much information and no more. His job is to produce only what it contains."

Dr. Frank Yates of the Rothamsted Experimental Station, and a student of Fisher, appropriately emphasized:

"Don't expect too much of statistics or the statistician. Don't for instance, expect every bit of statistical analysis to yield useful results, and don't be afraid of consigning the unprofitable bits to the wastebasket, or, at least to the filing cabinet. Don't, when you have collected a mass of numerical data which do not appear to be making any very clear statement, expect that the statistician will necessarily be able to reveal the hidden truth that has escaped you. He may be able to help you, but, equally, the data may just not be capable of revealing anything. Don't clutter up your scientific papers with details of arithmetic which are better left in the notebook. And, above all, obtain statistical advice at the planning stage, as well as after the results have been collected."

At this point, it seems appropriate to ask, "Are all tools available to the scientist?" These tools, in addition to those mentioned above, should include a more adequate academic program in mathematics and statistics for the undergraduate and graduate students in the subject-matter departments of our educational institutions. Special efforts are needed to adapt graduate courses in statistics to the needs and objectives of the graduate students concerned. This should include training in experimental design, sampling theory, and in supporting mathematics. In addition, some knowledge of the application of statistical theory should be made available.

However, scientists with a more extensive collegiate training in mathematics and statistics will not necessarily eliminate the need for the consulting statistician. Present-day research is getting more complex, requiring simultaneous evaluation of many variables, or the determination of significance of very small differences between treatments. That this can be done is made possible by more precise automatic instrumentation and the development of statistical techniques, as well as the use of electronic computer facilities.

The availability of a computer for research scientists aids in the development of more complex statistical and mathematical models. As a result,

experiments can be planned to give consideration to the simultaneous study of more variables in search of details of fundamental knowledge. Moreover, the computer has made possible the numerical solution of many difficult problems not formerly feasible. It permits new research to be started more quickly, based on the results of computations made available sooner. Studies that have taken years to complete with manual computations are now available much earlier. This permits scientists to continue studies, rather than spending time summarizing their results by hand. Thus, a scientific computing service for research scientists supplements the statistical consulting services and affords an opportunity for a broader application of statistical methods in order to permit more effective and efficient research programs. Here again, a clear delineation of the objectives of the experiment by the research will materially assist the programmer in developing the most efficient procedure for making the statistical analysis.

It should be emphasized that computers are good servants, but bad masters. Only wise use and proper control of computers will prevent inappropriate utilization of this important research tool.

Another aspect of providing statistical assistance for the scientist and perhaps as equally important is the effort necessary to keep the consulting statistician abreast of the developments in statistical theory and experimental design. The solution of this difficulty requires arrangements whereby these statistical consultants may be assigned to a college or university for a period of time. Alternatively, this need affords an opportunity for some department of statistics to offer seminar-type courses that permit the discussion of new statistical developments and the consideration of specific problems presented to the consultants by research workers.

Needless to say, the methods of making statistical and computing tools available to the scientist are many and varied. But if we expect to attain the most efficient research, more consideration must be given to these tools.

E. L. LECLERG

*Director (Retired), Biometrical Services
Agricultural Research Service
U.S. Department of Agriculture
Beltsville, Maryland*

Contributions of Agricultural Productivity to National Economic Growth

One of the important characteristics of this scientific age is the gradual realization that research to create new products and techniques can be a profitable economic investment. A corollary is that man, through science, has virtually unlimited capacity to amplify the output from the basic raw materials provided by nature. The world's greatest ultimate resource is the human mind and its ability to shape the materials of nature to improve economic living standards and real income.

This paper focuses on the returns from scientific investment in the agricultural sector. Some of the inferences, however, may have an even broader application.

Sources of Farm Productivity

In American agriculture, the aggregate food supply has expanded to meet a total demand that has increased 1.8 percent annually despite almost no increase in the aggregate volume of conventional inputs of farm land, labor, and capital since 1950. These conventional inputs, however, have increased in productivity because of the use of nonconventional factors, principally education and research.

Much the same increases in productivity due to technological and educational advancements have taken place in all sectors of our economy.

Gains in output per unit of conventional resources in U.S. agriculture are the direct result of adoption of new and improved machinery, fertilizers, seeds, pesticides, feeds, and management techniques. Specialization, large-scale operations and improved financial, legal, insurance and transportation facilities have contributed in a quite direct way to farm productivity. Basically, these direct sources of rising productivity are the result of nonconventional inputs, mainly an extensive program of education, which has helped considerably in creating the environment that made new technologies feasible. Education has shaped the goals and values of farmers, made them more profit conscious, made them seekers of cost-reducing innovations. Education has created the foundation for the skills, apparatus, and knowledge that make research economically feasible.

Traditionally, economists have concerned themselves with optimum allocation and accumulation of conventional capital, land, and labor inputs. In



a total sense, however, the optimum allocation of inputs cannot be judged without including education and research as production inputs. In other words, just as managers decide to invest in operating capital, machinery, or plants based on expected returns, so managers—or in the case of public funds, society as a whole—can do the same with the cost-versus-returns approach of investments in research and education.

Investment to raise the productivity of conventional farm and nonfarm resources through research and education tends to be a more roundabout process than typical capital investment. But the basic principles of investment still apply. In equilibrium—point of optimum allocation of inputs—the return on investment (and rate of growth) equals the discount people place on future versus present consumption. Investments that yield over, say, five percent are exploited, and those that yield less are shunned. This process among many individuals in the market theoretically leads to the determination of the interest rate which is a measure of investment yield opportunities and time preference for consumption. However, institutional restric-

tions, indivisibilities and uncertainties severely distort the process.

Rates of Return on Education and Research

Table 1 contains estimates of the contribution to national income in 1963 from agricultural productivity advances since 1910. National income in 1963 was \$476 billion. Only 3.7 percent of it originated in the farm sector. Assume that in 1963—as was true in 1910—35 percent of the U.S. population lived on farms. Further, assume that on the average as in 1963, persons on farms contribute \$1,310 per capita to national income and persons not on farms contribute \$2,617 per capita to national income. Then the national income would be \$68 billion (or 14 percent) lower in 1963 without the changes in agricultural productivity that have accrued from all sources since 1910. Estimates for recent years from Table 1 and other sources¹ suggest the changes stemming from greater farm productivity now accelerate national income by \$1–1.5

¹ Tweeten, Luther G. and Plaxico, James S., Long-Run Outlook for Agricultural Adjustments, *Journal of Farm Economics*, 46: 39–55, Feb. 1964.

TABLE 1.—APPROXIMATE CONTRIBUTION TO THE 1963 NATIONAL INCOME OF CHANGES IN U.S. AGRICULTURE SINCE 1910

Decade or year	Contribution to 1963 national income
	(Billion 1963 dollars)
1910-20	11.6
1920-30	12.8
1930-40	4.2
1940-50	19.5
1950-60	16.0
1961	1.5
1962	1.0
1963	1.5

Total contribution to 1963 national income since 1910.....68.1

billion each year. If each annual increment is \$1 billion and is permanent, the present value of accumulated future benefits from each annual change in productivity totals \$20 billion when discounted at five percent.

To this measure of gross returns we must compare the cost of raising productivity. The current annual public cost of agricultural research, extension, and vocational training totals approximately \$.5 billion. Private investment in research and development adds \$.3 billion.² The estimated annual expense for rural farm primary and secondary education is \$2.7 billion. The sum of these three costs to raise farm productivity is \$3.5 billion. Adding an additional \$3.5 billion Federal outlay to support farm prices and control or dispose of excess production brings the input value to \$7 billion.³ The cost of education in the nonfarm sector that contributes to agricultural productivity must also be included. Estimated on the basis of the non-

farm population engaged in supplying farm inputs, the cost may be \$2 billion. Other miscellaneous items such as higher education and roads add \$1 billion to inputs, which brings the grand total input volume to \$10 billion.

Given the present value of discounted future benefits totaling \$20 billion, the benefit-cost ratio is 2.0. Others have estimated rates of return of 100 percent or more on investment in farm technology.⁴ We caution that these estimates are very crude and do not adequately match inputs and resulting outputs of relevant periods. But even allowing for, say, a 50 percent overestimation (we speculate that the above data more likely tend to underestimate rather than overestimate gains), few uses of public or private funds would give as high a return. But this statement must not be construed to mean that all uses of funds to increase productivity will bring similar gains.

Allocating Limited Funds for Nonconventional Inputs

Because of the high return on investment in farm productivity, it is safe to conclude that further in-

² Projected from a 1953 estimate of \$140 million by Mighell, assuming the same trend in agricultural research as occurred in all types of private research. Cf. R. L. Mighell, *American Agriculture*, John Wiley and Sons, New York, 1955.

Research and development outlay in 1960 by agricultural chemical and farm machinery firms was \$114 million. Nestor E. Tarleckyj, *Research and Development: Its Growth and Composition*, National Industrial Conference Board, Inc., New York, 1963.

³ The assumption is that commodity programs to restrict farm output and maintain farm income would not have been necessary in the absence of public and private investment in education and research.

⁴ Heady, Earl O., *Agricultural Policy Under Economic Development*. Iowa State University Press, Ames, Iowa, pp. 600-601, 1962.

Griliches, H. Zvi, *Research Costs and Returns: Hybrid Corn*. *Jour. Polit. Econ.* 66: 419-431, Oct. 1958.

vestment will be judged desirable. However, funds available for such purposes are limited and the optimum investment in agricultural technology cannot be considered apart from the rate of returns on alternative uses of these limited funds. The optimum allocation of limited funds between investment in science in the farm and nonfarm sectors would be that where the rates of return on the marginal dollar of investment in each sector are equal.

Few estimates of rates of return on investment in education and research in the nonfarm sector are available. Ewell has estimated that the rate of return on research in the total economy averages 100 percent.⁵ This estimate, if broadly interpreted as a measure of return on investment in the nonfarm sector, is consistent with the return computed earlier for agriculture. The similarity of estimates provides no basis for concluding that a major immediate redistribution of expenditures between sectors would be desirable. Of course the estimates are not strictly comparable, and both may contain sizeable errors.

Long-run trends in funds for investment in education, research, and development between sectors depend on several factors. The rate of return on research is known only in retrospect, hence is not a very efficient allocator. However, expectations of returns may be of some importance. The fact that agriculture was one of the first major industries singled out for massive research emphasis is only partially explained by expectations of large economic gains from such outlays.

More important reasons for early emphasis on farm research may have been the market structure and size of the farm sector. The public reasoned that each individual farmer could not undertake a program of research. Farmers acting individually possessed neither the capital nor the equity to bear the consequences of uncertain returns on any one undertaking, or a market (production potential) sufficient to reap the gains from research. Where bigness counted, the government of a prosperous society no longer needed to spend all its product including taxes on direct, immediate needs. Hence, it found itself in a position to support research in agriculture—the nation's major industry.

Undoubtedly, public funds will continue to be a major source of support for research and development in all sectors—including business—because of the same reasons that individual farmers could not undertake the needed extensive research program.

Partially motivated by large payoffs from research in agriculture, private and public focus is now preoccupied with research as a productive investment of limited capital. This emphasis also is motivated by the improved methodology, trained personnel, and apparatus—electronic computers for example—that reduce the cost of research per unit of findings.

The rate of return on investment in research and development is expected to continue to be high as in the past. Other things being equal, initial investments utilize obvious opportunities and in general exploit areas where research returns are high. Further investments would be expected to reduce the benefit-cost ratio through the principle of diminishing returns.

But scale economies are important. In science, new investments feed and prosper on old breakthroughs. Bigger, more efficient apparatus and trained personnel more effectively use funds. The ubiquitous involvement in research insures that one effort may gain from insights gleaned in another. For these and other reasons, we believe the age of science will not soon reach a stage of diminishing returns and low productivity if growth is balanced.⁶ Rather, the age of science is cumulative. It has the potential for a vertical explosion in knowledge and its application along with the attendant gains for our national welfare.

Decline of Agricultural Research Funds

The decision by society to invest in farm productivity through support of agricultural research was motivated by a desire to improve the welfare of farmers. The decision was not directly motivated by prospects of a high economic return on research investment. Nor was it motivated by the prospect that farming would contribute to national economic growth through a relatively retarded income, heavy

⁶ A very great increase in funds for research without the necessary personnel (which require much time to educate) or apparatus would not be expected to bring satisfactory output at least in the short-run. It has been said, for example, that a major short-run increase in funds for space research would bring inflation to salaries and lead to waste, because the basic raw materials (well-trained scientists) are either not available or would be bid away from some equally productive use.

⁵ Ewell, R. H., Role of Research in Economic Growth, *Chemical and Engineering News*, Vol. 33, July 18, 1955.

outmigration, and a sharply declining share of the national population. These, of course, are symptoms of contributions to national economic growth that benefit society in total.

Public investment in education and research has been so successful that rural farm people as a proportion of the population declined from $19\frac{1}{20}$ ths in 1790 to about $1\frac{1}{20}$ th currently. Resources have moved out of agriculture at a staggering pace. Still, our ability to produce exceeds our ability to consume by 7 percent at current prices.⁷ This is sufficient capacity (insurance) at stable farm prices and commodity stocks for our society to meet its food and fiber needs without expanding resources or productivity for 3 years. Similarly, it represents sufficient capacity to sustain a drought that drops production 7 percent.

Society's tastes, as reflected by low income elasticities of demand for farm products, cause consumer income in a growing economy to be spent

largely for items produced off the farm. Because of the declining part of the farm sector in our national economy and the existing excess capacity in agriculture, it is not surprising to note that the proportion of investment in science is shifting to the nonfarm sector (table 2).

Future contributions from rising agricultural productivity to national growth through farm migration will be diminished. The current absolute rate of farm outmigration must decline or no persons will remain in agriculture. The tendency to diminish agricultural science returns from slackened migration from the farm will be offset to an undetermined extent by conventional capital savings and pressures to meet food needs of a population that doubles each 45 years.

In 1940, investment in scientific research and development in the farm sector accounted for 63 percent of all government expenditures, including that for defense and space. By 1964, this percentage had decreased to only 11.5 percent. Not much is known of the nongovernment allocation of research funds to agriculture. Table 3 suggests, however, that a major part of research and development

⁷ Tyner, Fred and Tweeten, Luther, Excess Capacity in U.S. Agriculture, *Agricultural Economics Research*, January, 1964. Cf. Luther Tweeten and Fred Tyner, Toward an Optimum Rate of Technological Change, *Journal of Farm Economics*, December, 1964.

TABLE 2.—FEDERAL GOVERNMENT EXPENDITURES FOR SCIENTIFIC RESEARCH AND DEVELOPMENT, 1940 TO 1963 ¹

Year	All Federal expenditures	All Federal expenditures (less defense, AEC, and space)	Farm		Nonfarm	
			Total expenditures	Percent of all Federal expenditures (less defense, AEC, and space)	Total expenditures	Percent of all Federal expenditures (less defense, AEC, and space)
	Million dollars	Million dollars	Million dollars	Percent	Million dollars	Percent
1940	74	46	29	63.0	17	37.0
1950	1,083	155	53	34.2	102	65.8
1955	3,308	219	73	33.3	146	66.7
1960	7,738	697	129	18.5	568	81.5
1962	10,373	1,027	166	16.2	861	83.8
1963	12,226	1,314	180	13.7	1,134	86.3
1964	14,979	1,622	186	11.5	1,436	88.5

¹ U.S. Department of Commerce, *Statistical Abstract of the United States* (1963), p. 544, and (1964), p. 542; and *Historical Statistics of the United States* (1957), p. 613.

TABLE 3.—SOURCES OF FUNDS FOR TOTAL RESEARCH AND DEVELOPMENT, UNITED STATES, 1945-1962

Year	Federal Government	Industry	Colleges and universities	Other nonprofit institutions ¹	Total funds
	<i>Percent of total</i>	<i>Percent of total</i>	<i>Percent of total</i>	<i>Percent of total</i>	<i>Million dollars</i>
1945	70	28	1	(²)	1, 520
1950	56	41	3	(²)	2, 870
1953-54	53	43	3	1	5, 150
1954-55	55	42	2	1	5, 620
1955-56	57	39	2	1	6, 390
1956-57	59	38	2	1	8, 670
1957-58	63	34	2	(³)	10, 100
1958-59	64	33	2	1	11, 130
1959-60	66	32	2	1	12, 680
1960-61	65	33	2	1	13, 890
1961-62 ⁴	65	32	2	1	14, 740
1962-63 ⁴	67	30	2	1	16, 420

¹ Includes State and local funds received by these institutions.

² Not available.

³ Less than 0.05 percent.

⁴ Preliminary

Source: U S. Department of Commerce, *Statistical Abstract of the United States* (1963), p. 543 and (1964), p. 541.

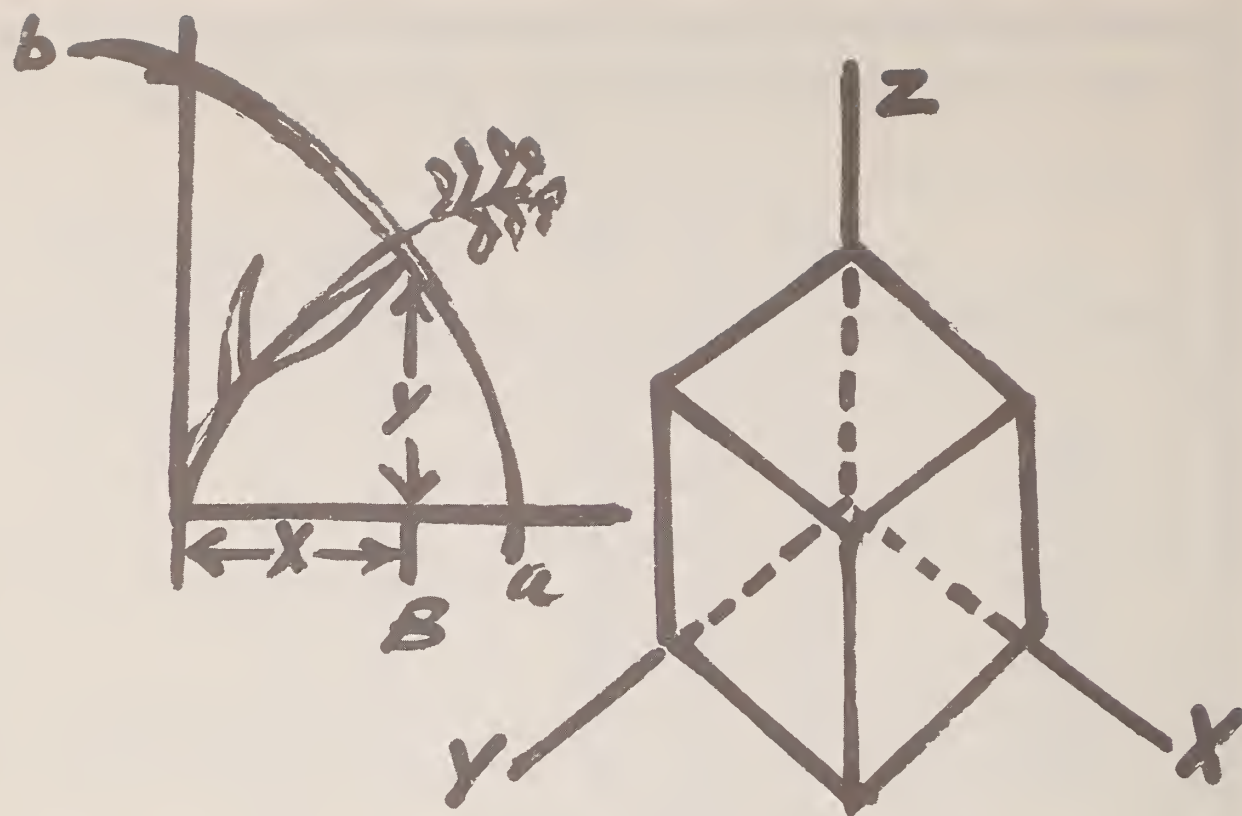
(two-thirds) is from government funds. Research and development financed by industry would be expected to focus on agriculture even less than do Federal funds. Hence, data in Table 2 represent the upper proportion of current research and development funds allocated to increase farm productivity.

Summary and Conclusions

The available data suggest that average returns are large on investments to raise the productivity of farm and (based on fragmentary data) the nonfarm sectors through education and research. What little data are available give no basis for expecting a major redistribution of funds for education and research between the two sectors at this time. In the longrun, however, the nonfarm sector will experience a secular increase in the proportion of such investment.

Education will continue to rest principally on public funds as expected. Scale economies, uncertainties, and divergence between private and social costs (or gains) will ensure a continued major role of public funds in research also. The fact that research is becoming more profitable—and necessary in many cases to meet competition—also ensures that private research investment will increase substantially. Because of traditional emphasis placed on private industry and efficiencies therein, private firms perhaps will perform an increasing segment of publicly-financed research and development. Yet it is an interesting observation that the principal future sources of economic growth—education and research—are not very efficiently allocated by the price mechanism. Rather, allocation of funds for science is based to a great extent on institutional forces. The impact of these trends on our economy and culture is indeed significant.

* * *



A GEOMETRIC APPROACH TO PLANT BREEDING

The present analysis is concerned with the intermediate ground between biochemistry and biophysics at the cellular level at one extreme and statistical inference concerning gene action on the other. This is not to decry either, since both are extremely useful, but to point out that there is a middle ground to this body of biological knowledge which can be a fascinating subject for investigation.

Sufficient evidence now is on hand to evaluate some segments of this work. No one denies the geometrical nature of complex characters such as yield, but many reject the usefulness of such an approach. This divergence of opinion is largely a matter of philosophical orientation. Some prefer to work with the chemistry of the gene, and some prefer to infer gene action through statistical treatment. Others prefer to make biological simplifications wherever advantageous before applying complex statistical analysis.

The arguments advanced in chapter I point out the relationship between the geometry of complex traits, such as yield, with types of heterosis and homeostasis. It is emphasized that the component approach is a venture into the understanding of the complex trait through increased knowledge of the sequential nature of the development of the plant

and the reaction of the components to environmental stresses.

* * *

Yield: A Geometrical Interpretation

Yield is a product; this is true whether it is yield of grain, hay, wool, eggs, saw logs, or fish worms. As such, it has a geometry. In the case of yield of oats, it may be represented geometrically as the volume of a rectangular parallelepiped ($W = XYZ$) with edges (X) the number of panicles per unit area, (Y) the average number of kernels per panicle, and (Z) the average kernel weight.

Such a representation is not just a play on words, but permits the establishment of several theorems which should clarify some of the objectives of selection for high yield. The plant breeder has long known that there are certain varieties which perform well over a wide area. Just how or why such a universal variety maintains its standing in the various plant communities is a most intriguing problem and one that is basic to plant breeding. The universal variety must either resist change, or adjust favorably to changes in environment. While the buffer may be both physiological and struc-

A recent publication from the Michigan Agricultural Experiment Station documents a rather unusual approach to certain aspects of plant breeding. Titled, "A Geometry of Plant Breeding," the bulletin was written by John E. Grafius of the Department of Crop Science. It presents a complete treatment of those aspects of plant breeding which are amenable to a geometric approach. Dr. Grafius points out that geometry serves only as a vehicle for better understanding of biology and not as an end in itself.

The report represents, in part, research undertaken during the author's sabbatic leave at the University of Birmingham and Cambridge University and sponsored by the Guggenheim Foundation and Michigan State University.

Review is privileged to reprint here selected passages of Dr. Grafius' report.

tural, the physiologic responses should find their ultimate expression in the physical components of yield. This is not to say that the physiological changes should be ignored, but that the metric changes in structure are easier to observe in the field and this aspect should be exploited first.

[At this point the author presents a series of theorems, tables and charts which serve to further illustrate and document the geometrical approach. Chapters 2 through 6 discuss other aspects of the topic; chapter 7, which follows, is reprinted in full.]

Practical Considerations

Plant breeders are the engineers of the biological real world. Their problems are primarily those of construction of superior genotypes for specific environments. While relying upon such sciences as genetics, physiology, pathology, cytogenetics, entomology, and morphology the field is distinct from any of these. The problems unique to plant breeding are the complexities. It is all very well to measure respiration on a dozen plants in the laboratory, but how does one make this reading on 2,000 plants in the field? Studies on selection involving a few traits in a controlled environment are enlightening, but how can one select for, say, twenty important traits simultaneously among thousands of lines when he can't even collect the data, let alone control the environment?

In contrast to the geneticist, the plant breeder frequently deals with more complex traits, greater numbers of traits, and an unstable environment. His rate of progress in the future is dependent upon

how well he can solve the problems attendant to these conditions. The situation is not all black. It is easy to forecast that much of the field data eventually will be taken electronically and processed directly without having to be recorded and sorted by human hands. Important as this step will be, it is over-shadowed by a tool which is available now. The plant breeder's one supreme advantage over the evolutionist is that he can construct the population in which he chooses to work.

Think for a minute what such a tool can mean. By constructing his population so that the means for a large number of traits approach an ideal, it should be possible to concentrate on selecting for the few traits which are out of focus with the ideal, acting on the assumption that those lines saved will tend to be satisfactory in other respects. Granted, linkage and high genetic variances may present obstacles, but construction of several populations for each ideal will enable one to work within the most favorable progenies. It is quite possible to choose parents so that the genetic variance for certain traits is low. This may sound like heresy, but when the population means approach the ideal for n traits then it is desirable that the range for some of these traits be narrow (low genetic variance) so that selection pressure on recalcitrant traits will result in varieties or lines which will be in focus with the ideal for all traits. Where linkage interferes with progress, several generations of random mating may help to secure new combinations.

Population building by the choice of parents

through the vector technique is a solution to the problem of dealing with many traits at one time. The problem of making laboratory measurements on a field scale is another, which fortunately is amenable to a similar approach. In general terms suppose a certain enzyme has been found to enable a plant to withstand competition for light. Suppose further that the higher the concentration of enzyme, the better the competitive ability. Obviously, other factors such as ability to compete for water or nutrients and a host of environmental variables could produce the same phenotypic response in the field so that it is important to know whether or not the enzyme is causing the observed response—among several thousand plants. At the present time it is impossible to obtain this kind of data.

The proposed way around should be apparent to the reader since it follows the same pattern. The steps are:

1. Observe a large number of putative parents for response to competition.
2. Select lines which show a strong response and those which are buffered and study these under controlled conditions to isolate causes.
3. Construct populations in such a way as to maximize chances of isolating the desired reaction in an acceptable phenotype.
4. Plant indicators as biological checks so that if the desired response does not take place in the check, then selection should not be carried out.
5. Select plants or lines from the population which have a favorable phenotypic response to competition, i.e., less sterility, less lodging, etc. The number of survivors should be reduced to a size which can be handled in the laboratory.
6. Measure the response of the survivors under controlled conditions. Chances are that at least some of the favorable phenotypic responses observed in the field will be due to the desired factor.

7. Recurrent selection via the vector method to concentrate the factor in a desirable phenotype.

Unstable Environments

The problem of unstable environments deserves special attention. Perhaps the best solution for this is to test under a wide variety of environments and then relate this information to the expected environments where a variety is to be released. The Canadians have initiated such a scheme. The use of biological indicators, i.e., standard varieties which respond to environmental stresses common to the area, is another means of characterizing seasons so as to know whether or not to select. However, it is quite evident that not only must we recognize the occurrence of genotype-environment interactions but we must know why. In many cases where the cause is known, the interaction ceases to be a problem. The problem of genotype-environment interaction in winterhardiness of barley ceased to be confusing once the cause of the interaction was recognized.

It is obvious that there are many different levels of why. The recognition of causes of winterhardiness i.e., the resistance to winter injury when the plants are hardened and dry or resistance when the plants are rehydrated, constitutes a level which is useful but not very sophisticated in the light of recent advances in this area. The recognition of components of other complex traits such as the components of yield is a useful biological subdivision. But this does not mean that the quest should stop here. The quest will continue. However, some means of integrating this new knowledge into the agricultural frame of reference must be found. Geometry is one convention which should aid in this ordering of knowledge of life processes.

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THE AUTHORS

GEORGE W. GORSLINE ("Computer Applications to Agricultural Experimental Data") is assistant professor of agronomy and chief consultant of the Computation Center at Pennsylvania State University. He received his B.S. degree from Virginia Polytechnic Institute in 1948, following which he was Extension county agent for 7 years in Pennsylvania. He was awarded his M.S. (1957) and Ph.D. (1959) degrees from Penn State. Dr. Gorsline's research deals chiefly with corn breeding and inheritance of quantitative economic characters, particularly yield, standability and mineral accumulation.

RUSSELL G. LYNCH ("Linguistic Barriers in Science Writing") was, until his retirement last year, a staff writer for the *Milwaukee Journal*. In his 42 years of service, he filled a variety of editorial posts, including 8 years as special reporter on natural resources for the *Journal*. He received the first MacQuarrie Award in 1958 for outstanding writing on conservation matters. In 1963 his series of articles about the public lands won the *Journal* a merit award from the Soil Conservation Society of America. He received the Thomas L. Stokes award for 1964 for articles on western water problems and national water pollution studies. He wrote the widely circulated booklet, *Our Growing Water Problems*, for the National Wildlife Federation. Since his retirement, Mr. Lynch has served as editorial consultant to public and semipublic agencies.

LUTHER G. TWEETEN ("Contributions of Agricultural Productivity to National Economic Growth") is associate professor of agricultural economics at Oklahoma State University. He received his B.S. degree (1954) and Ph. D degree (1962) from Iowa State University, and his M.S. degree (1958) from Oklahoma State University. In 1962, he joined the staff at Oklahoma State University as assistant professor and was appointed associate professor in 1963.

FRED K. HINES is research associate in agricultural economics at Oklahoma State University. He received his B.S. degree (1962) and M.S. degree (1964) from Oklahoma State University.

WOON H. JYUNG ("Pathways and Mechanisms for Foliar Absorption") is assistant professor of biology, University of Toledo, Toledo, Ohio. He received his B.S. degree in botany from Seoul National University, Korea, in 1957 and both his master's (1959) and Ph. D. (1963) in horticulture (physiology) from Michigan State University. After completing his graduate work, he held a postdoctoral research appointment at Michigan State for 1 year. Dr. Jyung is a member of both the American and Japanese Society of Plant Physiologists.

SYLVAN H. WITTWER ("Pathways and Mechanisms for Foliar Absorption") is professor of horticulture, Michigan State University. He received his B.S. degree from Utah State University in 1939 and his Ph. D. from the University of Missouri in 1943 where he was an instructor for 3 years. Dr. Wittwer received the Leonard H. Vaughn Award in vegetable crops in 1953, the AAAS-Campbell Award in 1957, the Michigan Chapter of Sigma Xi Junior Award for meritorious research in plant physiology in 1955, and the Distinguished Faculty Award at Michigan State in 1965.

JAMES G. ROSS ("Somatic Chromosome Reduction as a Tool in Plant Breeding") is professor of agronomy, South Dakota State University. He acquired his B.S. and M.S. degrees in Canada and in 1947 was awarded his Ph. D. in botany at the University of Wisconsin. He joined the South Dakota staff in 1947 as an assistant professor of agronomy. During 1958-59 he was a Guggenheim Fellow at Lund University, Sweden, where he worked on cytogenetic problems in sorghum.

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